THE GENERA OF ROSACEAE IN THE SOUTHEASTERN UNITED STATES *

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Subfam. ROSOIDEAE

About 520 species (excluding the apomictic complexes of *Alchemilla*, *Potentilla*, and *Rubus*) in 41 genera and eight tribes. Eleven genera representing seven tribes occur in the southeastern United States. Two, *Alchemilla* and *Duchesnea*, are introduced. *Kerria* and *Rhodotypos* may possibly be established locally in our area and are included in the key to genera (see discussion under *Neviusia*). Two genera, *Dalibarda* and *Neviusia*, are restricted to eastern North America, eleven to western North America, seven to Eurasia, four to Africa and Macaronesia, and three to South America. Twelve genera are largely of the North Temperate region; *Acaena* is circum-Antarctic. Tribe Adenostomateae includes a single genus with two species, *Adenostoma fasciculatum* Hooker & Arn., $2n = 18$, and *A. sparsifolium* Torrey, $2n = 18$, both from the Upper Sonoran Zone of California and Baja California (see Anderson, subfamily references, for a study of introgression in *A. fasciculatum*).

Base chromosome numbers in the tribes of Rosoideae are nine in the Kerrieae (*Neviusia* has counts of $2n = 14, 16, 18$); seven in the Ulmarieae (some aneuploidy); seven in the Rubeae; seven in the Fragarieae; seven in *Geum*, *Waldsteinia*, and *Coluria* and nine in the other genera of Dryadeae; eight in *Alchemilla* and seven in the remaining genera of Sanguisorbeae that have been examined cytologically; nine in the Adenostomateae; and seven in the Roseae.

SUBFAMILY REFERENCES:

ANDERSON, E. Introgression in *Adenostoma*. Ann. Missouri Bot. Gard. **41**: 339–350. 1954.

BESSEY, E. A. The comparative morphology of the pistils of the Ranunculaceae, Alismaceae and Rosaceae. Bot. Gaz. **26**: 297–313. *pl. 25*. 1898.

BRESINSKY, A. Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaisomen. Studien zur myrmekochoren Verbreitung von Samen und Früchten. Bibliot. Bot. **126**: 1–54. 1963.

CHOAY, E. Recherches anatomiques et physiologiques sur les Dryadées. 128 pp. *4 pls*. Paris. 1888.*

JACKSON, G. The morphology of the flowers of *Rosa* and certain closely related genera. Am. Jour. Bot. **21**: 453–466. 1934. [*Dalibarda*, *Dryas*, *Geum* *Rubus*, and *Waldsteinia*.]

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* Continued from volume 55, p. 332.

NESTLER, C. G. Monographia de *Potentilla*. 81 pp. + *11 pls*. Paris and Strasbourg. 1816. [Also *Dalibarda* and *Waldsteinia*.]

RYDBERG, P. A. A monograph of the North American Potentilleae. Mem. Dept. Bot. Columbia Univ. **2**: 1–221. *pls. 1–112*. 1898.

SCHAEPPI, H., & F. STEINDL. Vergleichend-morphologische Untersuchungen am Gynoeceum der Rosoideen. Bull. Soc. Bot. Suisse **60**: 15–50. 1950.

Tribe KERRIEAE Focke

5. **Neviusia** A. Gray, Mem. Am. Acad. Arts Sci. II. **6**: 374. *pl. 30*. 1858.

Deciduous shrubs with numerous slender, arching primary stems and short lateral branches; twigs terete, decurrently ridged from the nodes; buds small, solitary, sessile; leaf scars round-cordate to crescent-shaped, slightly elevated with 3, ± doubled bundle scars; indumentum of simple and, on the lower leaf surfaces, multicellular glandular trichomes. Leaves alternate, petiolate; blades simple, ovate with rounded or rarely cordate bases, acute to acuminate-attenuate apices, and usually doubly serrate margins; stipules free, setaceous, the lower part persistent as a small scale. Inflorescences few flowered, open, subumbellate corymbs terminating growth of the current season, flowering as the leaves expand; bracts small, linear. Flowers apetalous, about 2.5 cm. in diameter, perfect. Calyx without an epicalyx, the 5–7 lobes large, green, foliaceous, deeply toothed above the middle, reflexed at anthesis, persistent and enlarged somewhat in fruit, quincuncial in aestivation; floral cup flat, very short. Petals absent. Androecium of numerous stamens (usually more than 100) inserted in several whorls on the flat floral cup area; filaments white, long, slender, free to the bases, persistent, the inner shorter than the outer; nectar ring not discernible; anthers yellow, small, basifixed. Gynoecium of 2–5 superior and free carpels (opposite the calyx lobes when 5); styles as many as the carpels, free, terminal on the adaxial margins of the carpels, the lower part persistent on the fruit; stigmatic region a narrow vertical band on the adaxial surface of the styles; each carpel with a single anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit a greenish, drupaceous achene, the epicarp slightly fleshy, thin, the endocarp crustaceous. Seeds one per carpel, completely filling the achene; testa smooth, thin; embryo descending, completely surrounded by a layer of endosperm, the cotyledons plano-convex, the radicle superior, inflexed-accumbent. TYPE SPECIES: *N. alabamensis* A. Gray. (Named in honor of one of the original collectors, the Rev. Reuben Denton Nevius, 1827–1913.) — SNOW-WREATH.

One of our rarest shrubs, *Neviusia alabamensis*, the only species of the genus, was known for a long time only from the cliffs along the Black Warrior River above Tuscaloosa, Alabama; this species is now known from Tuscaloosa, Jackson, Madison, and Morgan counties, Alabama; Conway and Faulkner counties, Arkansas; and Butler County, Missouri. The type locality was evidently destroyed by blasting operations about the turn of

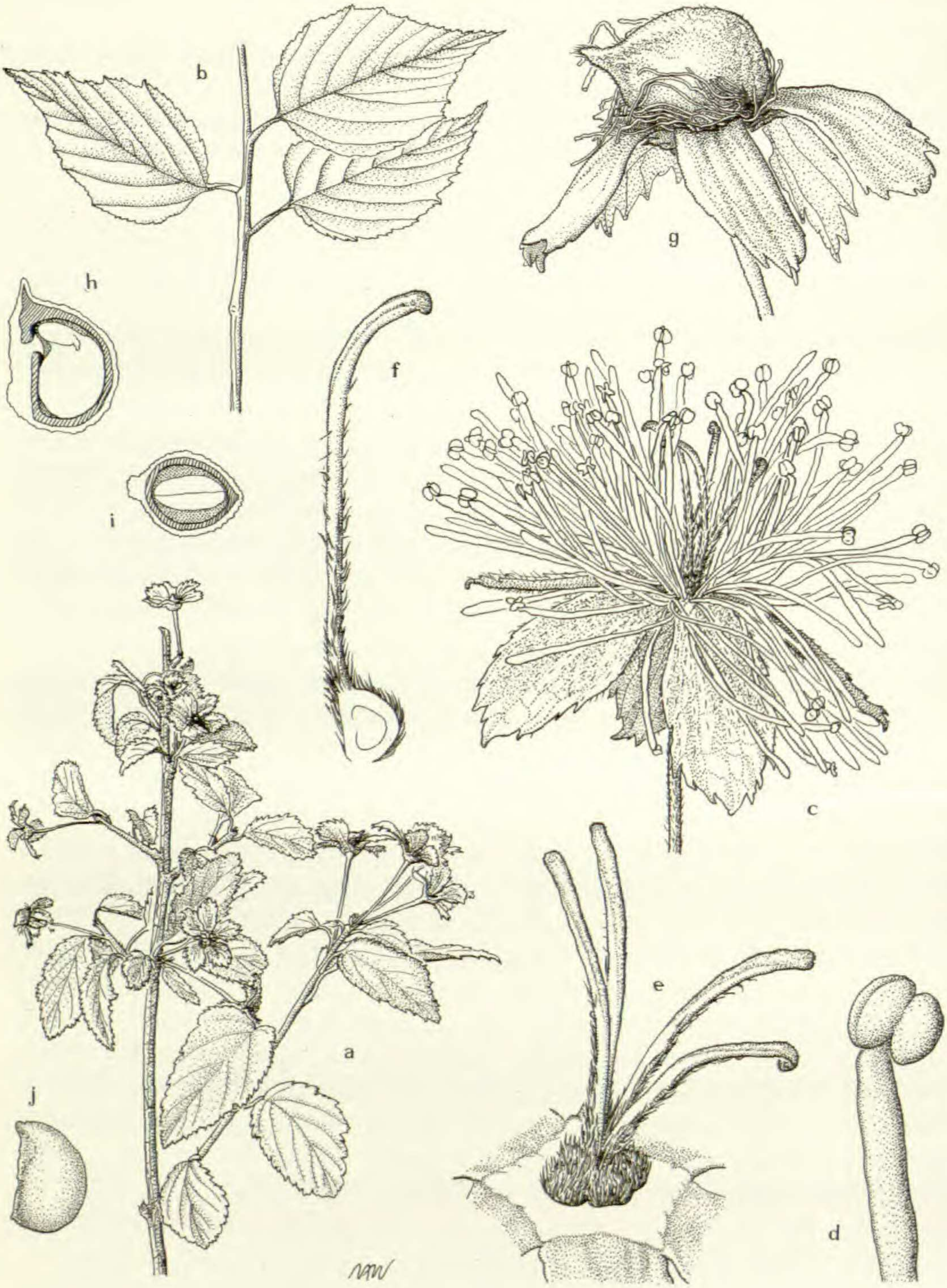

FIGURE 4. **Neviusia.** a–j, *N. alabamensis*: a, tip of long shoot with several lateral shoots in fruit, × 1/2; b, leaves of long shoot, × 1/2; c, flower — note numerous stamens, × 4; d, tip of stamen, × 20; e, central part of flower, stamens removed, to show gynoecium, × 8; f, carpel, ovary in vertical section (ovule nearly pendulous, micropyle superior) — note stigmatic band on adaxial surface of style, × 10; g, fruit, calyx lobes and filaments persistent, × 4; h, vertical section of fruit, epicarp (unshaded) slightly fleshy, endocarp (hatched) crustaceous, embryo surrounded by endosperm (stippled), × 4; i, same, in cross section, × 4; j, seed, × 4.

the present century, but populations still occur along both sides of the river in that vicinity. The Missouri record by Uphof seems certain, although later attempts to relocate his stations have been unsuccessful.

The substrata on which *Neviusia* has been reported are shale, limestone, and sandstone in Alabama, sandstone in Arkansas, and sandy loam in Missouri. All these are Carboniferous or sub-Carboniferous formations. Moore points out that all the known localities for *Neviusia* lie at the periphery of the Mississippi embayment of the old Gulf Coastal Plain and suggests that since this area has been above sea level since the late Paleozoic or early Mesozoic, *Neviusia alabamensis* might be an epibiotic, relatively old relict species, rather than a strict endemic of recent origin.

The chromosome number of *Neviusia* was first reported by Sax (1931) as $2n = 16$; he corrected this the next year to $2n = 18$, stating that the earlier count was an error since the chromosomes tend to clump. Baldwin confirmed Sax's later count, but Thomas & Deramus give the chromosome number of this species as $2n = 14$. The supposed relatives of *Neviusia*, *Kerria japonica*, and *Rhodotypos scandens*, have a reported chromosome number of $2n = 18$.

Tribe Kerrieae is composed of three monotypic genera, *Kerria* DC., *Rhodotypos* Sieb. & Zucc., and *Neviusia*. *Kerria japonica* (L.) DC. (flowers 5-merous, petals yellow, carpels 5–8) is native to central and western China and Kyushu, Shikoku, and Honshu islands, Japan. Commonly grown in North American gardens, this species perhaps has escaped locally from cultivation; Small reports *K. japonica* from eastern South Carolina, but Radford, Ahles, & Bell do not include the species in their *Flora of the Carolinas*. *Rhodotypos scandens* (Thunb.) Makino (*R. kerrioides* Sieb. & Zucc.) (leaves opposite, flowers 4-merous, petals white, carpels 4 and developing into shining, black, dryish drupes) is native to eastern Asia. Although *Rhodotypos* is commonly cultivated and is locally adventive in North America, the only possible record of this species in our area is from a single, supposedly wild plant, near the Guntersville Dam, Marshall County, Alabama, collected and communicated in 1969 by J. E. Butler, of New Hope, Alabama, to J. L. Thomas, who, in turn, relayed the information to us.

The phenolic constituents of the members of tribe Kerrieae are fairly well known (see Bate-Smith and Harborne, family references; Challice [1973], Maloideae references). Within subfam. Rosoideae, flavones are restricted to tribe Kerrieae. Ellagic acid, a compound universal in other Rosoideae, is lacking in *Neviusia*, *Kerria*, *Rhodotypos*, and *Coleogyne ramosissima* Torrey (southwestern North America; included in tribe Kerrieae by Schulze-Menz). Sorbitol, found throughout the Maloideae, Amygdaloideae, and Spiraeoideae, is restricted to tribe Kerrieae within subfam. Rosoideae. *Rhodotypos* differs from *Kerria* and *Neviusia* by the absence of leuco-anthocyanins. Thus, on chemical grounds a strong argument could be made for removing tribe Kerrieae from the Rosoideae. Morphologically, these three genera occupy a position somewhere between the Spiraeoideae and Rosoideae. Since detailed comparative studies have not been made, it seems best for now to follow Gray's alignment of these genera with the Rosoideae.

Neviusia alabamensis is hardy far to the north of its native range, and plants have survived in the coldest part of the Arnold Arboretum for many years. Although usually cultivated only as a novelty and rarely listed in nursery catalogues, the white stamens give plants of *Neviusia* in full bloom much the attractive aspect of *Fothergilla*, of the Hamamelidaceae. It deserves more horticultural attention. Unless carefully pruned, the plants can assume an unkempt appearance similar to their wild relatives growing on densely vegetated cliffs. Evidently, all plants in cultivation are derived from the populations along the Black Warrior River; it is quite possible that the other natural populations could produce more horticulturally desirable forms.

Information on pollination mechanisms is lacking, but the plants are evidently partly self-compatible since the sole plant of the species in cultivation at the Arnold Arboretum produces some fruit each year.

REFERENCES:

Under family references see BALDWIN, BATE-SMITH, BEAN, DIPPEL, REHDER, and SCHNEIDER.

ALEXANDER, E. J. *Rhodotypos kerrioides.* Addisonia **23**: 45, 46. *pl. 759.* 1958.

BEAN, W. J. Trees and Shrubs. Gard. Chron. III. **35**: 229, 230. 1904. [Good illustration of *N. alabamensis*; also see *Ibid.* **41**: 40, 41. *photo opposite 41.* 1907.]

FERNALD, M. L. Specific segregations and identities in some floras of eastern North America and the Old World. Rhodora **33**: 25–63. *pl. 204.* 1931. [*Neviusia*, 29.]

FOCKE, W. O. Die Keimung von *Kerria* und die natürliche Gruppe der Kerriae. Abh. Naturw. Ver. Bremen **12**: 343–345. 1892.

GRAY, A. *Neviusia*, a new genus of Rosaceae. Mem. Am. Acad. Arts Sci. II. **6**: 373–376. *pl. 30.* 1858.

HARPER, R. M. Notes on the distribution of some Alabama plants. Bull. Torrey Bot. Club **33**: 523–540. 1906. [*Neviusia*, 532.]

———. Economic botany of Alabama. Part 2. Catalogue of the trees, shrubs and vines of Alabama, with their economic properties and local distribution. Geol. Surv. Alabama Monogr. **9**. 357 pp. University, Alabama. 1928. [*Neviusia*, 194–196; photographs.]

HOOKER, J. D. *Neviusa* [sic] *alabamensis.* Bot. Mag. **111**: *pl. 6806.* 1885.

MOHR, C. Rare and little known trees and shrubs of Alabama. Trans. Mississippi Valley Hort. Soc. **2**: 216–219. 1884? *

———. Plant life of Alabama. Alabama ed. xii + 921 pp. *pls. 1–13*; *A, B.* Montgomery, Alabama. 1901. [Reprinted from Contr. U.S. Natl. Herb. **4**, with added letter, biography, and *pls. A, B*; *Neviusia*, 539, *pl. 4.*]

MOORE, D. M. *Neviusia alabamensis* in Arkansas. Rhodora **58**: 187–191. 1956.

MURBECK, S. Über staminale Pseudapetalie und deren Bedeutung für die Frage nach der Herkunft der Blütenkrone. Acta Univ. Lund. II. Sect. 2. **14**(25): 1–59. 1918. [*Neviusia*, 6–8, 50, 51, 58; illustration of staminal insertion of *Neviusia, Kerria, Rhodotypos.*]

POLLARD, C. L. A visit to the home of *Neviusia.* Pl. World **3**: 136, 137. 1900.

THOMAS, J. L., & R. DERAMUS. The chromosome number of *Neviusia alabamensis* Gray. Rhodora **66**: 274. 1964.

UPHOF, J. C. T. Das Vorkommen von *Neviusia alabamensis* Gray in Süden von Missouri. Mitt. Deutsch. Dendrol. Ges. **31**: 282, 283. 1921. [Illustration.]

———. Ecological relations of plants in southeastern Missouri. Am. Jour. Bot. **9**: 1–17. *pls. 1, 2.* 1922. [*Neviusia*, 7.]

Tribe ULMARIEAE Focke

6. **Filipendula** Miller, Gard. Dict. Abr. ed. 4, alph. ord. 1754.

Tall, rhizomatous, glabrous [or pubescent], perennial herbs; stems erect, hollow [or solid], grooved [angled or rounded], mostly unbranched below the inflorescences, the nodes somewhat swollen. Leaves aromatic, the basal ones quite large, imparipinnately compound, the leaflets incised and sharply toothed, the terminal leaflets palmately cleft, larger than the reduced or nearly absent lower leaflets, small leaflets frequently interspersed with larger leaflets along the rachis; cauline leaves similar, but becoming smaller and less compound toward the stem apices; stipules of the basal leaves adnate to the petioles, those of the cauline leaves free, large, asymmetrically reniform, clasping, incised. Inflorescences ebracteate, many flowered, ascending, paniculate corymbs terminating erect stems, the lateral inflorescence branches exceeding, and flowering after, the central ones; pedicels pink [or green]. Flowers small, 5-merous, perfect [or imperfect, the plants then dioecious]. Calyx without an epicalyx, often colored as the petals, deeply lobed, the segments reflexed at anthesis, persistent, valvate in aestivation; floral cup shallow [to nearly flat], free of the carpels, the upper part slightly thickened and fleshy. Petals pink [white, yellowish, or purple], spreading at anthesis, deciduous, about twice as long as the calyx lobes, shortly clawed [or not], the blades orbicular [to ovate] with slightly erose [or entire] margins, the bases auriculate [rounded or tapering]. Androecium of 10–40 (usually 15–20) stamens; filaments slender, equaling or exceeding the petals, deciduous, nearly hypogynous and inserted in several series on the short floral tube; anthers medifixed, deep pink [yellow or white], the anther sacs slightly separated, the connectives enlarged on the abaxial side. Gynoecium of 5–15 free, sessile or stipitate carpels in one whorl [the carpels sometimes spirally imbricated]; styles short, terminal on the adaxial margins of the carpels, bent above so the stigmas face outward laterally; stigmas comparatively large, capitate-discoid, terminal; each carpel with 2 anatropous ovules pendulous from the upper adaxial part of the wall, the micropyle superior. Fruit elongate, flattened, indehiscent, one-seeded, few [to all] carpels of a flower developing into fruit; seed not filling fruit, the seed coat thin, the radicle superior. (Including *Ulmaria* Miller, 1754; *Filipendula* and *Ulmaria* first united, under the former name, by Adanson, Fam. Pl. **2**: 295. 1763.) LECTOTYPE SPECIES: *Spiraea Filipendula* L. = *F. vulgaris* Moench; see B. L. Robinson, Rhodora **8**: 204. 1906; also see P. A. Rydberg, N. Am. Fl. **22**: 266. 1908. (Name from Latin, *filum*, a thread, and *pendulus*, hanging, after the tuberous roots of *F. vulgaris* that seem suspended from thin roots.)

A small genus of North Temperate and Subarctic regions composed, according to Shimizu, of 15 species in three subgenera and four sections. *Filipendula rubra* (Hill) Robinson occurs in eastern North America, *F. occidentalis* (S. Watson) Howell in northwestern Oregon, two species in Eurasia, and the remaining species primarily in eastern Asia.

Filipendula rubra (*F. lobata* (Jacquin) Murray), queen-of-the-prairie, had an aboriginal distribution from Pennsylvania to Minnesota, southward to North Carolina, Georgia, Kentucky, Illinois, and Missouri, but has escaped from cultivation northward and eastward to New York, New England, and Nova Scotia. This plant, a tall perennial herb with hollow stems, large leaves, palmately lobed leaflets, showy inflorescences of pink flowers, and glabrous, short-stipitate, straight carpels, prefers moist habitats such as meadows, wet prairies, low woods, and bogs. Shimizu places this species, along with seven species of northeastern Asia, in subg. ULMARIA (Miller) Juz. sect. SCHALAMEYA Juz. and notes that *F. rubra* and *F. palmata* (Pall.) Maxim. are geographically vicarious species. *Filipendula occidentalis* is quite different and belongs to the monotypic subg. HYPOGYNA Shimizu. Two European species, *F. vulgaris* (*F. hexapetala* Gilib., nom. illegit.), dropwort, of subg. FILIPENDULA, and *F. Ulmaria* (L.) Maxim., queen-of-the-meadow, have escaped from cultivation to the north of our area.

Because of the general aspect of plants of *Filipendula* species, their small flowers with several free carpels in one whorl on a flat receptacle, and the fruits resembling follicles (although they are indehiscent), this genus was referred by early authors to the Spiraeoideae. However, interruptedly compound leaves (the basal ones with the stipules adnate to the petioles), such as those of *Filipendula*, are common in tribes Dryadeae and Sanguisorbeae of subfam. Rosoideae but do not occur in the Spiraeoideae. The fruits are one-seeded and indehiscent, as in most Rosoideae. The base chromosome number of seven in *Filipendula* is common in the Rosoideae, but is virtually absent from the Spiraeoideae. A glucoside, spiraeoside (quercetin-4′ glucoside) occurs in *F. vulgaris* and *F. Ulmaria* but not in species of *Spiraea*; its possible occurrence in other Rosoideae has evidently not been checked. *Thriphragmium filipendulae*, a rust fungus of tribe Phragmideae, parasitizes *F. vulgaris*; related fungi are known from numerous Rosoideae but few Spiraeoideae. All these data indicate that *Filipendula* is best placed in the Rosoideae.

Reported chromosome numbers in the genus are *Filipendula kamtschatica* (Pall.) Maxim., $2n = 14–18, 28, 28–42$; *F. palmata*, $2n = 14, 15$; and *F. yezoensis* Hara (as *F. koreana*), $2n = 16$. Such disparities in base chromosome numbers and ploidy levels both within and between species suggest that a cytotaxonomic study of the genus would be illuminating. An odd-diploid chromosome number of 15 was listed by Maude for English horticultural material of *F. vulgaris* (as *Spiraea Filipendula*). Darlington inferred that the situation in this species paralleled that experimentally observed in *Campanula persicifolia* in which a metacentric or acrocentric chromosome misdivided through the centromere producing two telocentric chromosomes; "in *Spiraea Filipendula* in England it [the odd-diploid number] is found in every individual. The species has become a true-breeding hybrid in respect of a structural change in the chromosomes. . . ." Baker & Baker, however, dispute this hypothesis on the basis of their observation of $n = 7$ and $2n = 14$ in numerous plants of *F. vulgaris.*

REFERENCES:

Under subfamily references see SCHAEPPI & STEINDL; under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHITTENDEN, HEGI, HUBER (1961–1966), RICKETT, ROSS-CRAIG, and WOOD.

BAKER, H. G., & I. BAKER. The cytotaxonomy of *Filipendula* (Rosaceae) and its implications. Am. Jour. Bot. **54**: 1027–1034. 1967. [*F. vulgaris* and *F. Ulmaria*, both $2n = 14$.]

BARANOV, A. I. Contributions to the study of *Filipendula palmata* (Pall.) Maxim. and similar Far Eastern species. Bot. Jahrb. **79**: 521–525. 1960.

DARLINGTON, C. D. Chromosome botany and the origins of cultivated plants. ed. 2. xvi + 232 pp. London. 1963. [*Filipendula*, 14, 49.]

HÖRHAMMER, L., R. HÄNSEL, & W. ENDRES. Über die Flavonglykoside der Gattungen *Filipendula* und *Spiraea*. Arch. Pharm. **289**: 133–140. 1956. [*F. Ulmaria*, *F. vulgaris*, and 58 spp. of *Spiraea*.]

LEBÈGUE, A. Embryogénie des Rosacées. Développement de l'embryon chez le *Spiraea Ulmaria* L. Compt. Rend. Acad. Sci. Paris **228**: 1243–1245. 1949. [= *F. Ulmaria*; development of the embryo similar to that of *Geum urbanum*.]

MAUDE, P. F. Chromosome numbers in some British plants. New Phytol. **39**: 17–32. 1940. [*Filipendula*, 31, *fig. 21*.]

MEEHAN, T. *Spiraea lobata*. Meehans' Monthly **2**: 145, 146. *pl. 10*. 1892. [= *F. rubra*; colored plate.]

MOREVA, T. A. Dynamics of growth of the green stuff and accumulation of tannins of meadowsweet, *Filipendula Ulmaria* (L.) Max. (In Russian.) Acta Inst. Bot. Acad. Sci. URSS. 5. Mater. Rudes Pl. **4**: 269–285. 1956.

ROBINSON, B. L. *Filipendula rubra*, a new binomial. Rhodora **8**: 202–204. 1906.

SAUNDERS, E. R. On the gynaecium of *Filipendula Ulmaria* Maxim. and *Filipendula hexapetala* Gillib.: A correction. Ann. Bot. **49**: 848–852. 1935. [Refutes an earlier conclusion (Ann. Bot. **41**: 609, 610. 1927) that each ovary is composed of 2 carpels, one sterile and one fertile.]

SAVILE, D. B. O. Parasite relationships and disposition of *Filipendula*. Brittonia **20**: 230, 231. 1968. [The rust fungus found on *F. vulgaris* is closely related to those restricted to Rosoideae.]

SERGIEVSKAYA, E. V. Subgenus *Ulmaria* Moench of genus *Filipendula* Adans. on USSR territory and distribution of its species. 178 pp. Israel Program for Scientific Translations, Jerusalem. 1968.* [Translated from the Russian original of 1965.]

SHIMIZU, T. Taxonomical notes on the genus *Filipendula* Adans. (Rosaceae). Jour. Fac. Textile Sci. Tech. Shinshu Univ. **26**: Ser. A. 10: 1–31. 1961. [Complete taxonomic treatment of genus.]

YAPP, R. H. *Spiraea Ulmaria* L., and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. **26**: 815–870. *pls. 81–83*. 1912. [= *F. Ulmaria*; a study of the spatial and temporal distribution of foliar indumentum.]

Tribe RUBEAE Dumort.

7. Rubus Linnaeus, Sp. Pl. 1: 492. 1753; Gen. Pl. ed. 5. 218. 1754.

Mostly armed erect to trailing shrubs or scramblers from rootstocks or creeping stems, rarely herbaceous; shoots mostly biennial, those of the first year's growth (primocanes or, in older American and in European literature, turions) from buds at or below ground level, bearing leaves along their length, buds in the axils of these leaves producing lateral branches with leaves and flowers the next year, the cane usually dying after fruit matures (the whole second-year stem called a floricane); reproducing vegetatively by root or stem suckers or rooting stem tips; armature of the stems, inflorescence branches, petioles, and calyx lobes of variously shaped and sized prickles or bristles (acicles) or absent; indumentum of simple and/or sessile or stalked glandular trichomes, the density variable. Leaves deciduous or persistent through winter, those of the first and second year's growth often quite different, simple (mostly lobed), ternately trifoliolate, palmately compound with 5–7 leaflets, imparipinnate with 5–7 [or more] leaflets [or bipinnate or partly tripinnate]; leaflets toothed and often lobed, sessile to short or long petiolulate, the central leaflet often larger than the others; stipules linear, small to conspicuous, free or adnate to the base of the petiole, persistent or caducous. Flowers solitary or inflorescences determinate, simple or compound cymes, "racemes," or "panicles." Flowers usually showy, 5-merous, perfect [or imperfect, the plants then dioecious]. Calyx without an epicalyx, the lobes elongate, with acute or tapering-acuminate apices, ascending to reflexed at anthesis and in fruit, valvate in aestivation, persistent; floral cup short, nearly flat; nectar ring usually prominent. Petals white or rarely pink, elliptic to spathulate or orbicular, shorter than to exceeding the calyx lobes [or absent]. Androecium of many stamens inserted at the edge of the floral cup, the outer longer than and dehiscing before the inner ones; filaments slender; anthers sometimes pubescent. Gynoecium of numerous free carpels on a nearly flat to cylindrical receptacle; styles slender or somewhat clavate, terminal, commonly deciduous; stigmas discoid or slightly 2-lobed; each carpel with 2 collateral or superposed, anatropous ovules pendulous from an adaxial placenta, the micropyle superior. Fruit of many red to black (rarely white, yellow, or orange) 1-seeded drupelets on a dry or spongy, often elongated receptacle, the drupelets falling individually or coalescent and either falling from the receptacle as a unit or with it; stones hard, variously textured; seeds filling the stones; embryo small, the radicle superior. Base chromosome number 7. (Including *Rubacer* Rydb. and *Oreobatus* Rydb.) LECTOTYPE SPECIES: *R. fruticosus* L.; see N. L. Britton & A. Brown, Illus. Fl. No. U.S. Canada ed. 2. 2: 275. 1913.[5] — BLACKBERRY, DEWBERRY, RASPBERRY.

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[5] Later the same year, Rydberg (N. Am. Fl. 22: 429) listed *R. idaeus* L. as the type species. Hitchcock & Green (Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 1929) say: "The type-species of the genus *Rubus* is undoubtedly *R. fruticosus,* but this name has fallen into disuse as it has been used in different senses by different authors. It therefore seems preferable to choose *R. caesius* L. as the standard species."

Perhaps 700 or more species found nearly throughout the range of the family, the taxonomy of some subdivisions of the genus notoriously difficult. *Rubus* is particularly diverse morphologically in eastern Asia and South America and, to a lesser degree, in North America. Major concentrations of species (mostly the abundant forms of subg. RUBUS) occur in North America and Europe. Basic taxonomic works on *Rubus* are those of Sudre (1908–1913, Europe), Focke (1911–1914, world-wide revision), and Bailey (1941–1949, North America); unfortunately, the subgeneric classification and nomenclature of each of these works are largely independent of the others. Gustafsson's account of the European blackberries is a major contribution toward an understanding of that group.

Eleven subgenera, excluding *Dalibarda*, can be recognized; five widespread ones occur in eastern North America (three in our area). Three subgenera are confined to Asia and the western parts of the Americas, two are essentially restricted to South America, and subg. DALIBARDASTRUM is of eastern Asia.

Subgenus ANOPLOBATUS Focke (stems erect, unarmed; bark peeling or flaking; leaves entire, palmately lobed; styles somewhat clavate; receptacle nearly flat) is represented with us by *Rubus odoratus* L., $2n = 14$, flowering raspberry. This species occurs in shaded areas such as along the edges of woods, stream banks, and roadsides from Quebec and Nova Scotia to Michigan and Wisconsin, southward to New England, New York, Pennsylvania, the Virginias, Ohio, and Indiana, and in the mountains to North Carolina, Tennessee, and Georgia. The plant is a handsome shrub with large leaves (often 30 cm. wide) and rose-like, magenta flowers. The drupelets are reddish, densely pubescent apically and abaxially, only slightly fleshy, and scarcely edible; they fall from the receptacle either individually or in groups. The length of glandular trichomes on the pedicels and veins of the lower leaf surfaces and the density of nonglandular trichomes on the leaf blades is variable; Fassett distinguished seven forms based largely on these characters. Similar patterns of variation are found in the closely related, white-flowered *R. parviflorus* Nutt., $2n = 14$, thimbleberry, which occurs in western North America from Alaska to New Mexico and northern Mexico and disjunctly in the regions around the northern Great Lakes (northeastern Minnesota and adjacent Ontario, northern Wisconsin, northern Michigan and the Keweenaw Peninsula, and the Bruce Peninsula). *Rubus odoratus* and *R. parviflorus* evidently do not occur sympatrically. Other related species occur in western North America, Central America, and Japan.

Subgenus IDAEOBATUS Focke (stems erect, often arching, armed with prickles; petals [in ours] scarcely or not exceeding the calyx lobes; drupelets separating from the receptacle), raspberries, is primarily of temperate

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Most European authors today use *R. fruticosus* L. only in an aggregate sense for practically all of sect. *Rubus*, indicating that the name is based on two elements (*R. plicatus* Weihe & Nees and *R. ulmifolius* Schott f.) that belong to different subsections (see Heslop-Harrison in Valentine *et al.*, family references). Watson (1958) takes *R. ulmifolius* as the type species.

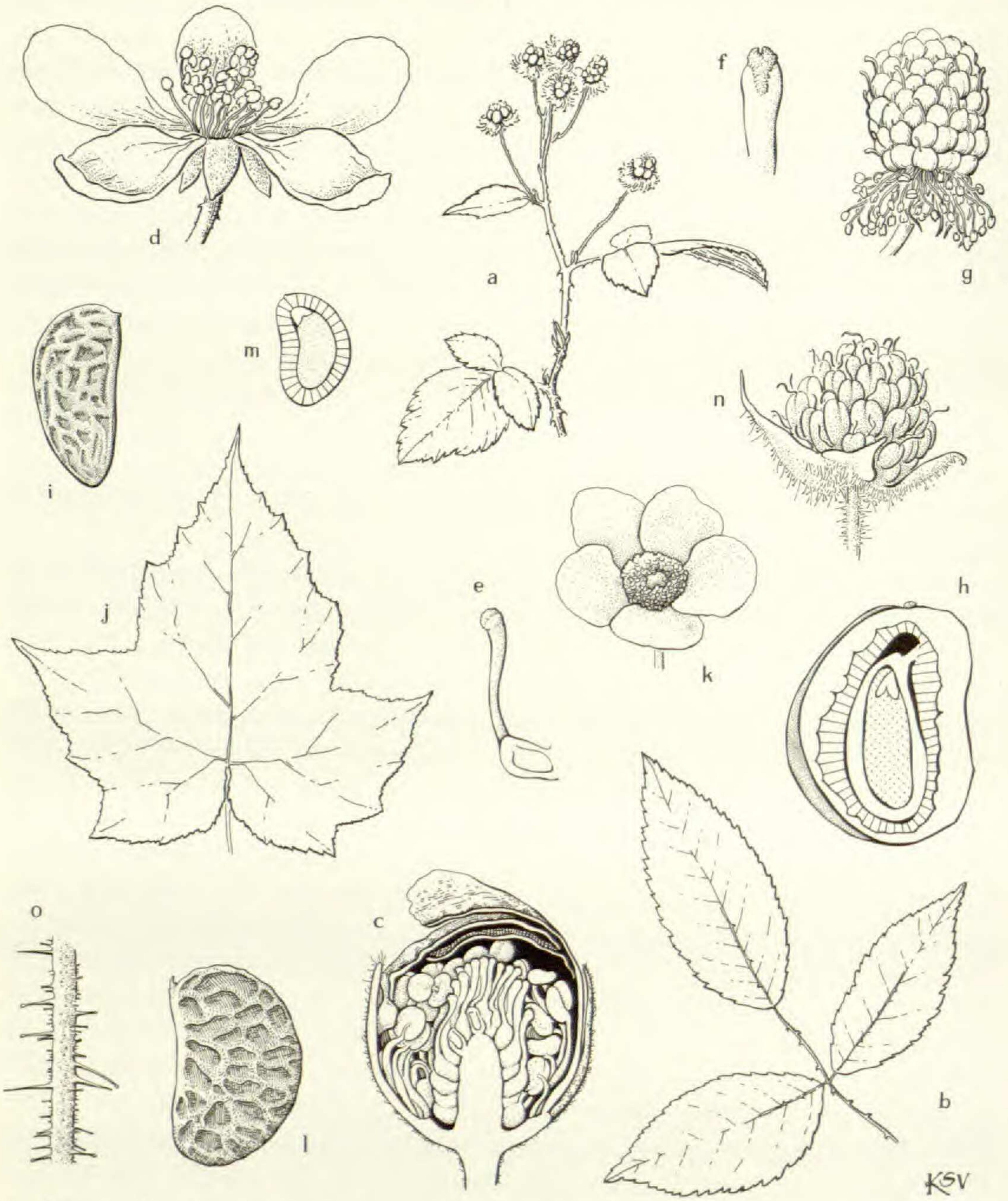

FIGURE 5. **Rubus** subg. **Rubus** (a–i), subg. **Anaplobatus** (j–m), and subg. **Idaeobatus** (n, o). a–i, *R. betulifolius*: a, tip of floricane with young infructescence, × 1/2; b, leaf of primocane, × 1/2; c, vertical section of flower bud, calyx lobes, petals, and stamens inserted at edge of nearly flat floral cup, carpels borne on cylindrical receptacle, × 6; d, open flower, × 2; e, carpel, ovule in section to show pendulous ovule, × 12; f, tip of style with stigma, × 25; g, nearly mature fruit, note persistent stamens, × 2; h, developing drupelet in section, fleshy outer layer unshaded, hard endocarp wall hatched, endosperm even-stippled, embryo sac unshaded [endosperm absorbed and embryo filling nutlet at maturity], × 12; i, endocarp from mature fruit, × 10. j–m, *R. odoratus*: j, leaf of floricane, × 1/2; k, flower at anthesis, × 1/2; l, endocarp from mature fruit, × 12; m, endocarp in vertical section, wall hatched, radicle unshaded, cotyledon stippled, × 6. n, o, *R. idaeus* subsp. *melanotrachys* (*R. strigosus*): n, mature fruit, × 2; o, detail of pedicel to show bristles and simple and glandular trichomes, × 6.

and subtropical Asia, and to a lesser degree, East and South Africa. Relatively few species occur in Europe, North America, and Australia. Bailey (Sp. Batorum, 859) says "Taxonomically the raspberries are the most difficult group of North American brambles."

Rubus idaeus L. (drupelets red; canes erect, not rooting at the tips; petals about equaling the calyx lobes), red raspberry, $2n = 14$ (polyploid in some cultivars), is variable particularly in the shape and size of the leaflets and calyx lobes and in the presence or absence, distribution, and size of prickles, bristles, stipitate-glandular trichomes, and eglandular trichomes. Several segregate species are sometimes recognized (see Hara, Hitchcock *et al.*, and Hultén [family references], Fernald, and Rozanova). The taxonomic treatment of Hara, who recognized one circumpolar species with several subspecies is followed here. Subspecies *idaeus* (inflorescences without glandular trichomes and bristles; drupelets coherent and falling as a unit) is a taxon of Europe and western Asia which Fernald contended is indigenous to the Dakotas and the Magdalen islands of Minnesota. It is commonly cultivated in much of North America and has escaped locally in some areas. Plants native to North America (Labrador to Alaska, southward to New England, Pennsylvania, the mountains of Virginia and North Carolina, Ohio, Indiana, Missouri, Nebraska, Wyoming, and Arizona) and much of eastern Asia have prominent stipitate-glandular trichomes on the young canes and inflorescence branches and drupelets that fall individually; these are distinguished as subsp. *melanolasius* Focke (including *R. strigosus* Michx., *R. sachalinensis* Lévl., *R. idaeus* var. *aculeatissimus* Regel & Tiling). Fernald distinguished five varieties in eastern North America; plants in our area correspond to var. *canadensis* Richardson. Varieties of the red raspberry of commerce are derived from either *R. idaeus* subsp. *idaeus* or subsp. *melanolasius*, or from hybrids between them (see Roemer & Rudorf, family references).

Rubus occidentalis L., black raspberry, $2n = 14$, a shrub with glaucous, arching canes that root at the tips, purple-black (rarely yellowish) drupelets, and petals shorter than the calyx lobes, has a broad distribution, Quebec to North Dakota and eastern Colorado south to Georgia, Arkansas, and Oklahoma. This species and *R. idaeus* subsp. *melanolasius* occasionally hybridize (*R.* × *neglectus* Peck) when they are sympatric. *Rubus leucodermis* Douglas ex Torrey & Gray, $2n = 14$, is a related species of Pacific North America. The various forms of the cultivated black raspberry are derived from *R. occidentalis*. Two species of eastern Asia are locally naturalized in our area: *R. phoenicolasius* Maxim. (canes, petioles, pedicels, and calyx lobes densely covered with long-stalked glandular trichomes; calyx lobes connivent around the red fruit), wineberry, $2n = 14$, and *R. illecebrosus* Focke (flowers and fruits quite large; canes annual), strawberry-raspberry, $2n = 14$.

Subgenus Rubus (subg. *Eubatus*) (petals longer than calyx lobes; drupelets retained on the deciduous or persistent receptacle), blackberries and dewberries, is one of the taxonomically more difficult groups in the North Temperate Zone. The European blackberries have been studied extensively (see particularly Gustafsson and Haskell). It is hypothesized that during the interglacial period of the late Pliocene or early Pleistocene there were a number of diploid, sexually reproducing species in Europe. As the glaciers moved southward, these self-incompatible species were at a disadvantage as the numbers of individuals became smaller and physically isolated from one another. Self-compatible, auto- or allopolyploids that were much better adapted to conditions during and after glaciation arose. Most of the diploid species became extinct. Recessive genes for apomixis were brought together by polyploidy and segregation, and as the glaciers retreated, the apomicts proliferated in the newly opened, barren habitats. It is these apomictic plants of hybrid origins and unknown parentage that are the dominant brambles in Europe today. Since apomixis in *Rubus* is facultative and pseudogamous, variation can result from the production of occasional sexual hybrids and, at least with respect to germination and seedling growth, from pseudogamously produced endosperm.

Detailed studies of North American species are lacking, but the situation here may be somewhat analogous to that in Europe. Some species are diploid or tetraploid and sexually reproducing, while others are polyploid and apomictic. The effect of Pleistocene glaciation on variability in subg. RUBUS in North America is unknown, but much of the variation may be of rather recent origin. As the lands were cleared for cultivation, species that were previously isolated perhaps came together and hybridized, as is presumably the case in *Crataegus* and *Amelanchier*. The taxonomic confusion within subg. RUBUS in North America will remain until a study that integrates gross morphology, cytology, embryology, and genetics is made.

Plants of subg. RUBUS in eastern North America are variable, particularly in growth habit; the number, disposition, and shape of leaflets; the morphology and distribution of spines, bristles, and glands; the pubescence of the leaves; and the type of inflorescence. In the preparation of herbarium specimens, it is necessary to collect both floricanes and primocanes and to take notes on the habit of the plant and whether the canes root at the tip or not. Taxonomic treatments of the subgenus vary widely: Bailey recognized about 400 species in America north of Mexico; Davis *et al.*, just under 200 in eastern North America; Fernald (Gray's Manual, ed. 8), nearly 200 in northeastern North America; Gleason (New Britton & Brown Illus. Fl. No. U.S. Canada), 15, including "collective species"; and Radford *et al.* (Man. Vasc. Fl. Carolinas), 15 in North and South Carolina. It is beyond the scope of this paper (or any other at present) to sort out the taxonomic problems in our area, but a few comments are in order.

All species of this subgenus in eastern North America belong to sect. MORIFERI sensu Focke (1910–1914). American botanists prefer to divide this group into numerous sections. Bailey recognized nine sections with species indigenous to North America; eight of these are largely confined to eastern North America, while sect. URSINI is restricted to the western United States. The sections in our area are: sect. HISPIDI Rydb. (rank assigned by Bailey), groundberries, dewberries, represented with us only by *R. hispidus* L. in the mountains and Coastal Plain of North and South

Carolina; sect. VEROTRIVIALES Bailey, southern dewberries, nearly confined to the Southeast; sect. FLAGELLARES Bailey, dewberries, widespread and taxonomically complex, the collective species *R. Enslenii* sensu Gleason mostly southern in distribution; sect. CUNEIFOLII Bailey, sand blackberries, mostly of the Coastal Plain and Outer Piedmont from Connecticut to Florida; sect. CANADENSES Bailey, smooth blackberries (a glandless and nearly thornless counterpart of the next section), mostly northern in distribution, occurring southward in the mountains to Georgia; sect. ALLEGHENIENSES Bailey, high bush blackberries, including many blackberries of northeastern North America, mostly in the mountains in our area; and sect. ARGUTI Rydb. (rank assigned by Bailey), high bush blackberries, widespread, exceedingly variable, and including the commonest southeastern blackberries.

The base chromsome number in *Rubus* is seven. Most species of subg. IDAEOBATUS are diploid and polyploidy (mostly autoploidy) has evidently played only a minor role in the evolution of this group. Most European species of subg. RUBUS are tetraploid, with relatively few diploids or hexaploids; triploids and pentaploids are quite rare. The North American species are more complex cytologically. All ploidy levels from diploid to 12-ploid occur; diploids, triploids, tetraploids, and hexaploids occur most commonly. Some species evidently have several ploidy levels. *Rubus ursinus* Cham. & Schlecht., of the Pacific Northwest, has reported chromosome numbers of $2n = 42, 56, 63, 70, 77$, and 84, the last the highest number known in the genus.

REFERENCES:

Under subfamily see JACKSON and SCHAEPPI & STEINDL. Under family references see BEAN, BUNTING, CHUTE, DEVADAS & BECK, DIPPLE, FREE, GUSTAFSSON, HARA, HEGI, HUBER (1961–1966), HULTÉN (1958, 1971), JESSEN, LÖVE & LÖVE, LUBBOCK, REHDER, ROBERTSON, ROEMER & RUDORF, ROSS-CRAIG, SCHNEIDER, STEPHENS, TAYLOR, VINES, and WOOD. Because of the great number of papers dealing with the breeding and commercial cultivation of *Rubus*, many references have been omitted; this list contains primarily basic taxonomic works, summary papers, and recently published titles.

AALDERS, L. E., & I. V. HALL. A cytotaxonomic survey of the native blackberries of Nova Scotia. Canad. Jour. Genet. Cytol. **8**: 528–532. 1966.

ALDOUS, S. E. Food habits of chipmunks. Jour. Mammol. **22**: 18–24. 1941. [Raspberries and thimbleberries important foods.]

BAILEY, L. H. Species batorum. The genus *Rubus* in North America (north of Mexico). I. Gentes Herb. **5**: 1–65. 1941; II. *Hispidi. Ibid.* 66–125; III. *Setosi. Ibid.* 128–198; IV. *Verotriviales. Ibid.* 200–228; V. *Flagellares. Ibid.* 230–422. 1943; VI. *Cuneifolii. Ibid.* 424–461; VII. *Canadenses. Ibid.* 464–503. 1944; VIII. *Alleghenienses. Ibid.* 506–588; IX. *Arguti*, European species introduced. *Ibid.* 590–856. 1945; X. *Idaeobatus, Anoplobatus. Ibid.* 858–918. Index to volume 5, 919–932. Addendum I. Chromosome studies in *Rubus* (by J. EINSET). *Ibid.* **7**: 181–192. 1947; Species studies in *Rubus. Ibid.* 193–349. Addendum II. *Rubus* studies — review and additions. *Ibid.* 480–526. 1949.

BAMMI, R. K., & H. P. OLMO. Cytogenetics of *Rubus*. V. Natural hybridization between *R. procerus* P. J. Muell. and *R. laciniatus* Willd. Evolution **20**: 617–633. 1966.

BARNOLA, P. Recherches sur le déterminisme de la basitonie chez le ronce (*Rubus fruticosus*). (English summary.) Beitr. Biol. Pflanzen **47**: 469–480. 1971.

BERGER, A. The systematic botany of edible brambles. Pp. 23–85. *In*: U. P. HEDRICK, *et al.*, The small fruits of New York. xi + 614 pp. *Frontisp. 94 pls.* 33rd Annual Rep. New York State Agr. Exper. Sta. Albany. 1925.

BERGER, X. Untersuchungen über die Embryologie apomiktischer *Rubus*bastarde. Bull. Soc. Bot. Suisse **63**: 224–266. *pls. 4, 5.* 1953.

BLANCHARD, W. H. *Rubus* of eastern North America. Bull. Torrey Bot. Club **38**: 425–439. 1911. [Concludes that 8 spp. include perhaps 90% of the blackberries.]

BOIVIN, B. Études batologiques. II. Sous-genre *Idaeobatus* Focke. Bull. Soc. Bot. France **102**: 237, 238. 1955.

BRITTON, D. M., & J. W. HULL. Mitotic instability in *Rubus*. Jour. Hered. **47**: 205–210. 1956.

CHRISTEN, H. R. Untersuchungen über die Embryologie pseudogamer und sexueller *Rubus*arten. Bull. Soc. Bot. Suisse **60**: 153–198. *pls. 1, 2.* 1950.

CLAUSEN, J., D. D. KECK, & W. M. HIESEY. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from the Madiinae. Carnegie Inst. Wash. Publ. **564**: vii + 1–174. *4 unnumbered pls.* 1945. [Amphiploids in the genus *Rubus*, 104–116.]

CRAIG, D. L. Studies on the cytology and the breeding behavior of *Rubus canadensis* L. Canad. Jour. Genet. Cytol **2**: 96–102. 1960.

CRANE, M. B. Reproductive versatility in *Rubus*. I. Morphology and inheritance. Jour. Genet. **40**: 109–118. 1940. [For part II, see THOMAS.]

———. The origin of new forms in *Rubus*. II. The loganberry, *R. loganobaccus* Bailey. *Ibid.* **40**: 129–140. *pl. 5.* 1940. [For part I, see below; for part III, see THOMAS.]

——— & C. D. DARLINGTON. The origin of new forms in *Rubus*. I. Genetica **9**: 241–277. 1927.

——— & P. T. THOMAS. Reproductive versatility in *Rubus*. III. Raspberry-blackberry hybrids. (With an appendix by C. D. DARLINGTON.) Heredity **3**: 99–107. *figs. 1, 2.* 1949. [For part I, see CRANE; for part II, see THOMAS.]

DAVIS, H. A., & Mrs. H. A. DAVIS. Collecting *Rubus* in the Upper South. Castanea **20**: 32, 33. 1955.

DAVIS, H. A., A. M. FULLER, & T. DAVIS. Contributions toward the revision of the *Eubati* of eastern North America. I. Castanea **32**: 20–37. 1967. II. *Setosi. Ibid.* **33**: 50–76. 1968. III. *Flagellares. Ibid.* 206–241. IV. [*Verotriviales, Canadenses, Alleghenienses.*] *Ibid.* **34**: 157–179. 1969. V. *Arguti. Ibid.* 235–266. VI. *Cuneifolii. Ibid.* **35**: 176–194. 1970.

DAVIS, W. H. Apomixis, hybridization, and speciation in *Rubus*. Castanea **23**: 52–55. 1958.

DOWRICK, G. J. Biology of reproduction in *Rubus*. *Nature* **191**: 680–682. 1961. [". . . apomixis in its commonly accepted sense, is not an important reproductive mechanism in tetraploid forms of *Rubus*. The production of maternal-like progeny, though superficially simulating apomixis, depends solely on the formation of reduced egg cells."

———. Breeding systems in tetraploid *Rubus* species. Genet. Res. **7**: 245–253. *pls. 1, 2.* 1966.

EINSET, J. Chromosome studies in *Rubus*. Gentes Herb. **7**: 181–192. 1947.

———. Apomixis in American polyploid blackberries. Am. Jour. Bot. **38**: 768–772. 1951.

FASSETT, N. C. Mass collections: *Rubus odoratus* and *R. parviflorus*. Ann. Missouri Bot. Gard. **28**: 299–368. *pls. 9–12.* 1941.

FERNALD, M. L. *Rubus idaeus* and some of its variations in North America. Rhodora **21**: 89–98. 1919.

———. Critical plants of the upper Great Lakes region of Ontario and Michigan. Rhodora **37**: 272–301. *pls. 363–375.* 1935. [Includes *R. parviflorus*.]

FOCKE, W. O. Species Ruborum. Monographie generis *Rubi* prodromus. Bibliot. Bot. **72**: 1–223. 1910, 1911; **83**: 1–274. 1914. [The basic taxonomic work for the genus.]

GERLACH, D. Befruchtung und Autogamie bei *Rubus caesius*. (English summary.) Biol. Zentralbl. **84**: 611–633. 1965.

GUSTAFSSON, Å. The origin and properties of the European blackberry flora. Hereditas **28**: 249–277. 1942.

———. The genesis of the European blackberry flora. Lunds Univ. Årssk. II. Sect. 2. **39**(6): 1–200. 1943.

HASKELL, G. The history, taxonomy and breeding system of apomictic British *Rubi*. Pp. 141–151. *In*: J. G. HAWKES, ed., Reproductive biology and taxonomy of vascular plants. 183 pp. *Frontisp.* Oxford. 1966. [Includes references to earlier papers.]

HESLOP-HARRISON, Y. Natural and induced rooting of the stem apex in *Rubus*. Ann. Bot. II. **23**: 307–318. 1959.

HODGDON, A. R., & F. STEELE. Glandularity in *Rubus allegheniensis* Porter. Rhodora **64**: 161–168. 1962.

——— & ———. *Rubus* subgenus *Eubatus* in New England: a conspectus. Rhodora **68**: 474–514. 1966.

HUDSON, J. P. Effects of environment on *Rubus idaeus* L. I. Morphology and development of the red raspberry plant. Jour. Hort. Sci. **34**: 163–169. 1959. [Good review of the vegetative life history; for part II, see WILLIAMS.]

JENNINGS, D. L. Some genetic factors affecting fruit development in raspberries. New Phytol. **70**: 361–370. *pl. 1.* 1971.

———. Some genetic factors affecting the development of endocarp, endosperm and embryo in raspberries. *Ibid.* **70**: 885–895. 1971.

KATO, N. On the variation of nodal types in the woody plants. 2. A contribution to the nodal anatomy. 2. Jour. Jap. Bot. **42**: 161–168. 1967. [Includes *R. Sieboldii*, 165–167.]

KEEP, E. Accessory buds in the genus *Rubus* with particular reference to *R. idaeus* L. Ann. Bot. II. **33**: 191–204. *pls. 1–3.* 1969.

LARSSON, E. G. K. Experimental taxonomy as a base for breeding in northern *Rubi*. Hereditas **63**: 283–351. 1969.

MANDRIK, V. Y., & Y. P. PETRUS. Differentiation of seedbud, development of female gametophyte and embryogenesis in *Rubus idaeus* L. and *Rubus caesius* L. (In Ukranian; English summary.) Ukrain. Bot. Zhur. **28**: 469–476. 1971.

MARKARIAN, D., & H. P. OLMO. Cytogenetics of *Rubus*. I. Reproductive behavior of *R. procerus* Muell. Jour. Hered. **50**: 131–136. 1959.

OREDSSON, A. Drawings of Scandinavian plants. *17–20. Rubus* L. subg. *Rubus*. Bot. Not. **122**: 1–8. 1969; *21–24. Ibid.* 153–159; *25–28. Ibid.* 316–321;

29–32. Ibid. 449–456; *33–36. Ibid.* **123**: 1–7. 1970; *37–40. Ibid.* 213–219; *41–44. Ibid.* 363–370; *17–44.* Key to *Rubus* subg. *Rubus. Ibid.* 447–454.

PERCIVAL, M. S. Observations on the flowering and nectar secretion of *Rubus fruticosus* (agg.). New Phytol. **45**: 111–123. 1946.

PETRAKHILEV, I. M. Intergeneric hybrids of raspberries. (In Russian.) Priroda **1958**(8): 109–111. 1958.

PRATT, C., & J. EINSET. Development of the embryo sac in some American blackberries. Am. Jour. Bot. **42**: 637–645. 1955.

———, ——— & R. T. CLAUSEN. Embryology, breeding behavior and morphological characteristics of apomictic, triploid *Rubus idaeus* L. Bull. Torrey Bot. Club. **85**: 242–254. 1958.

REEVE, R. M. Fruit histogenesis in *Rubus strigosus*. I. Outer epidermis, parenchyma, and receptacle. Am. Jour. Bot. **41**: 152–160. 1954. II. Endocarp tissues. *Ibid.* 173–181.

ROUSI, A. Variation among populations of *Rubus idaeus* in Finland. Ann. Agr. Fenniae **4**: 49–58. 1965.*

ROYEN, P. VAN. The genus *Rubus* (Rosaceae) in New Guinea (Sertulum Papuanum XV). Phanerogamarum Monographiae 2. 126 pp. Lehre. 1969.

STEELE, F., & A. R. HODGDON. Hybridization of *Rubus hispidus* and *R. setosus.* Rhodora **65**: 262–270. 1963.

——— & ———. Hybrids in *Rubus* subgenus *Eubatus* in New England. *Ibid.* **72**: 240–250. 1970. [See correction on p. 547.]

SUDRE, H. *Rubi* Europae vel monographia iconibus illustrata Ruborum Europae. 305 pp. *215 pls.* Paris. 1908–1913.

TAMMISOLA, J., & A. RYYNÄNEN. Incompatibility in *Rubus arcticus* L. Hereditas **66**: 269–277. 1970.

THOMAS, P. T. Reproductive versatility in *Rubus*. II. The chromosomes and development. Jour. Genet. **40**: 119–128. 1940. [For part I, see CRANE.]

———. The origin of new forms in *Rubus*. III. The chromosome constitution of *R. loganobaccus* Bailey, its parents and derivatives. *Ibid.* **40**: 141–155. *pl. 6.* 1940. [For part II, see CRANE.]

THOMPSON, M. M. Cytogenetics of *Rubus*. II. Cytological studies of the varieties "Young," "Boysen," and related forms. Am. Jour. Bot. **48**: 667–673. 1961. III. Meiotic instability in some higher polyploids. *Ibid.* **49**: 575–582 1962.

TOPHAM, P. B. Fertility in crosses involving diploid and autotetraploid raspberries. I. The embryo. Ann. Bot. II. **31**: 673–686. 1967. II. Fruit and seed development. *Ibid.* 687–697.

VAARAMA, A. Cytology of hybrids between Pacific *Rubi ursini* types and an eastern blackberry. Am. Jour. Bot. **40**: 565–570. 1953.

VIRDI, B. V., & G. W. EATON. Embryo sac and early embryo development in the salmonberry (*Rubus spectabilis*). Canad. Jour. Bot. **47**: 1891–1893. 1969.

WALDO, G. F., & G. M. DARROW. Origin of the Logan and the Mammoth blackberries. Jour. Hered. **39**: 98–107. 1948.

WATSON, W. C. R. Handbook of the *Rubi* of Great Britain and Ireland. xi + 274 pp. Cambridge, England. 1958.

WEBER, H. E. Die Gattung *Rubus* L. (Rosaceae) im nordwestlichen Europa. Phanerogamarum Monographiae **7**. vii + 504 pp. Lehre. 1972.

WILLIAMS, I. H. Effects of environment on *Rubus idaeus* L. II. Field observations on the variety Malling Promise. Jour. Hort. Sci. **34**: 170–175. 1959. [For part I, see HUDSON.]

8. **Dalibarda** Linnaeus, Sp. Pl. 1: 491. 1753; Gen. Pl. ed. 5. 217. 1754.

Low, unarmed perennial herbs with the aspect of a stoloniferous *Viola*; rhizomes slender, with internodal roots. Leaves often evergreen, borne along the length of the rhizomes and sometimes in lax to ± condensed rootstocks on the rhizomes, simple, long petiolate, the blade rounded-cordate with crenate margins; stipules small, linear, deeply divided, free. Flowers solitary on axillary pedicels, heteromorphic: petaliferous, morphologically perfect flowers that rarely set fruit, and apetalous, "cleistogamous," fertile ones. Petaliferous flowers in the axils of leaves; calyx lobes 5, rarely 6, divergent, unequal, at least the outer ones apically 3-toothed; floral cup short; petals 5, white, elliptic, spreading, slightly exceeding the calyx lobes; androecium of ca. 50 exserted stamens inserted in several series at the apex of the floral cup, the filaments slender, white, the anthers about 5 mm. long; gynoecium of 5–10 villous carpels, usually not setting fruit. Apetalous flowers produced mostly from rosettes and from tips of rhizomes; pedicels not exceeding the petioles; calyx lobes 5, erect, inclosing the stamens and carpels, the outer ones apically 3-toothed; floral cup short; petals absent; androecium of 5–10 stamens, the anthers about 3 mm. long; gynoecium of 5–10 villous carpels on a flat receptacle, the styles terminal on the adaxial margin of the carpels, deciduous, the stigmatic region a band decurrent on the adaxial surface of the style, each carpel with 2 anatropous ovules pendulous from an adaxial placenta. Fruits of 5–10 nearly dry, light-colored drupelets inclosed by the calyx lobes; the exocarp slightly fleshy, pubescent, the mesocarp hard, slightly wrinkled longitudinally; seed nearly filling the carpel wall, the coat thin; embryo spathulate, the radicle superior, slightly bent. TYPE SPECIES: *D. repens* L. (Name commemorating Thomas François Dalibard, 1705–1799, French botanist.) — DEW DROP, FALSE VIOLET, ROBIN-RUN-AWAY.

A monotypic genus of eastern North America. *Dalibarda repens*, a distinctive species of moist or dry woods, bogs, and swamps, ranges from Quebec, Ontario, northern Ohio, Michigan, and Minnesota, south to New England, New Jersey, and Pennsylvania and in the mountains to West Virginia and North Carolina. In our area it is known only from bogs in Transylvania Co., North Carolina, where it is probably a relict from the last glacial period. Surprisingly little is known about this interesting plant; not even its chromosome number has been determined. The apetalous flowers appear to develop mostly before the petaliferous ones. The carpels of the petaliferous flowers seem to be normal, but they rarely set fruit; pollen of these flowers is evidently viable.

Linnaeus (Gen. Pl. ed. 5) allied this species with *Rubus Chamaemorus* L. and later (Sp. Pl. ed. 2. 708. 1762) included it in *Rubus* as *R. Dalibarda* (L.) L. Focke established *Rubus* subg. DALIBARDA for *R. Dalibarda*, also including *R. lasiococcus* A. Gray (British Columbia to California), *R. pedatus* J. E. Sm. (northwestern North America), *R. Fockeanus* S. Kurz (China and the Himalayas), and *R. Gunnianus* Hooker (Tasmania). Bailey maintained the genus *Dalibarda* and referred *R. lasiococcus*, *R. peda-*

tus, and six other species to *Rubus* subg. CYLACTIS, a somewhat heterogeneous group of mostly semiherbaceous northern species.

REFERENCES:

Under subfamily references see JACKSON and NESTLER; under family references see CHITTENDEN, CHUTE, and RICKETT.

BAILEY, L. H. The standard cyclopedia of horticulture. ed. 2. vol. 1. xxiv + 1200 pp. *frontisp.* New York. 1928. [*Dalibarda*, 961.]

———. Species Batorum. The genus *Rubus* in North America (north of Mexico). I. Gentes Herb. 5: 1–64. 1941. [*Dalibarda*, 25.]

FOCKE, W. O. Species Ruborum. Monographie generis Rubi prodromus. Bibliot. Bot. **72**: 1–223. 1910, 1911; **83**: 1–274. 1914. [*Rubus* subg. *Dalibarda*, 13–17.]

SMITH, J. E. Plantarum icones hactenus ineditae. vi + 75 pp. *pls. 1–75.* 1789–1791. [*Rubus Dalibarda*, *pl. 20.*]

Tribe FRAGARIEAE Dumort.

9. **Fragaria** Linnaeus, Sp. Pl. 1: 494. 1753; Gen. Pl. ed. 5. 218. 1754.

Perennial, rosulate herbs with simple [or compound], scaly crowns terminating underground rhizomes, spreading and forming colonies by stolons that root and produce plantlets at the nodes; principal roots several, coarse, the secondary roots fibrous and numerous. Leaves radical, with 2/5 phyllotaxy, trifoliolate or simple in the inflorescence [rarely all simple], long petiolate; leaflets deeply serrate at least apically, sessile to short petiolulate; stipules adnate to the bases of the petioles, membranaceous, persistent and forming scales on the crowns. Inflorescences usually one to few per crown, of rather loose, long pedunculate, few to several-flowered cymes, sometimes becoming racemiform; bracts conspicuous, the larger ones often foliaceous. Flowers perfect or partly to wholly imperfect and the plants then variously polygamodioecious. Calyx with an epicalyx, the epicalyx lobes narrower than the calyx lobes, both erect or reflexed at anthesis, persistent, valvate in aestivation; floral cup saucer-shaped, free of the carpels, a nectar ring absent. Petals 5 [to 9], white to pinkish, spreading, deciduous, orbicular to obovate, the margins slightly erose or undulate, the bases shortly clawed, inserted at the edge of the floral cup, imbricate. Androecium of usually 20–35 stamens in multiples of 5 and in 3 whorls, sometimes some or all reduced to staminodia; filaments unequal in length, basally dilated and fused to form a disk that lines the floral cup; anthers yellow, sometimes opening under tension throwing pollen onto the stigmas. Gynoecium of many free carpels on a hemispheric to conical receptacle that enlarges in fruit; styles inserted adaxially near the bases of the carpels, persistent; stigmas terminal, discoid; each carpel with one anatropous ovule ascending from the middle of the locule, the micropyle inferior. Accessory fruits red (infrequently white), fleshy, juicy, sweet and fragrant, subtended by the calyx and epicalyx, the entire fruits falling from the plants. Achenes brownish, minute, numerous, dry, crustaceous, superficial or sunken into

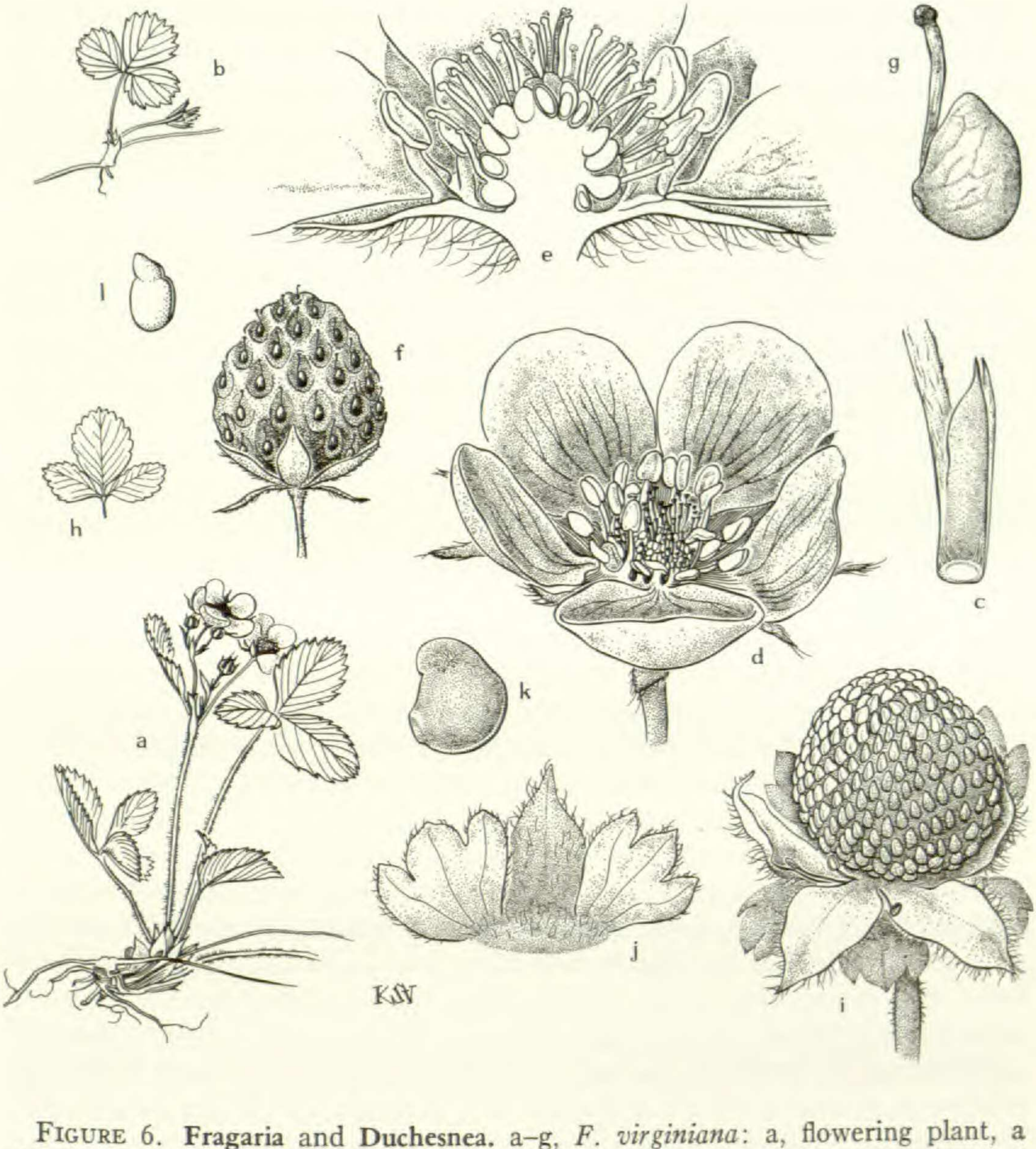

FIGURE 6. **Fragaria** and **Duchesnea.** a–g, *F. virginiana*: a, flowering plant, a stolon (pubescent) to right of crown, × 1/2; b, young plantlet on stolon, × 1/2; c, base of petiole showing adnate stipules, × 3; d, perfect flower, × 3; e, vertical section of flower, petals and stamens attached at edge of nearly flat floral cup, carpels on an elongated receptacle, × 6; f, accessory fruit, achenes in pits on fleshy, enlarged receptacle, × 1; g, side view of achene, style nearly basal, persistent, × 12. h–l, *D. indica*: h, leaf, × 1/2; i, fruit, calyx and epicalyx lobes persistent, styles deciduous, × 2; j, portion of floral cup with 2 trilobed epicalyx lobes and one entire calyx lobe, × 3; k, achene, attachment point of style (deciduous) at notch to upper left, × 12; l, embryo, oriented as in the achene, × 12.

shallow pits, persistent on the enlarged receptacles; embryo nearly filling the achene, spathulate, the radicle inferior, straight. Base chromosome number 7. LECTOTYPE SPECIES: *F. vesca* L.; see P. A. Rydberg, N. Am. Fl. 22: 356. 1908. (Name from *fraga,* the Latin name for the strawberry; the adjectival form was used by Linnaeus in reference to the fruit's fragrance.) — STRAWBERRY.

A natural assemblage of more than a dozen species primarily of the North Temperate Zone, but also indigenous (mostly at higher elevations) to Mexico, Central America, South America from central Chile southward to Patagonia, and Hawaii. Species and cultivars have been introduced into most of the world's temperate regions. Three species (and nine subspecies) occur in North America, two in our area. The species, often difficult to distinguish, can be placed in four groups that largely correspond to chromosomal ploidy level and geographical distribution. There are about nine diploid species ($2n = 14$) (all except *Fragaria vesca* confined to the Old World), with *F. vesca* and *F. viridis* Duchesne distributed throughout most of Europe, three species in Japan, and four species in the Himalayas. There are only two tetraploid species ($2n = 28$), *F. moupinensis* (Franchet) Cardot and *F. orientalis* Losinsk., both of eastern Asia, and only *F. moschata* Duchesne, of Europe, is hexaploid ($2n = 42$). *Fragaria virginiana* Duchesne (North America), *F. chiloënsis* (L.) Duchesne (California to the Aleutians; Chile and Argentina; Hawaii), and *F. iturupensis* Staudt (Iturup, Kuril Islands) are octoploid species with $2n = 56$. The nomenclature used below is based on that of Staudt (1962), in an important and rather widely accepted paper that unfortunately does not give descriptions, synonymy, or complete geographical ranges for the subspecific taxa.

Fragaria vesca L. (inflorescence often racemiform with unequal primary branches; calyx lobes spreading or reflexed after flowering; achenes superficial on the fruit), $2n = 14$, is circumboreal in distribution, occurring throughout Europe, in northern Asia, northern Africa, eastern and western North America, and Mexico. This species evidently is represented with us only by the occurrence of *F. vesca* subsp. *americana* (Porter) Staudt (*F. americana* Porter) in the rich woodlands of Watauga County, North Carolina. This subspecies, which differs from the typical form by its more slender habit, thinner, pale green leaves, and sparser, more or less appressed indumentum, is found in eastern North America from the Gaspé Peninsula southward to upland Virginia and northwestern North Carolina, and along the northern edges of the prairies to British Columbia. The primary range of subsp. *vesca* is Eurasian, but it is supposedly indigenous to Newfoundland and eastern Quebec, and it has been introduced into the northeastern United States. Staudt (1962) recognized two subspecies of *F. vesca* in the western United States, subsp. *bracteata* (Heller) Staudt and subsp. *californica* (Cham. & Schlecht.) Staudt. He suggested that the Mexican and Guatemalan populations (often called F. *mexicana* Schlecht. or *F. Gillmanii* Clinton) may conform to *F. vesca* subsp. *vesca* f. *semperflorens*

(Duchesne) Staudt. It appears that subsp. *americana* is more closely related to subsp. *vesca* than to either subsp. *bracteata* or *californica*.

Fragaria virginiana Duchesne has a very wide range: Newfoundland and the Hudson Bay region, to British Columbia, the Yukon, and Alaska, southward in the west to Montana, Colorado, New Mexico, and California, and in the east to Georgia, Alabama, Texas, and the midwestern states. This variable species, set apart by its low, slender habit, usually symmetrical umbellate cymes, small flowers and fruits, connivent calyx lobes, and achenes that are in pits on the accrescent receptacle, is an octoploid with $2n = 56$. Several subspecies, varieties, and segregate species, based largely on pubescence differences, have been proposed; further study of the variations and how they can be reflected best in a taxonomic scheme is needed. Four subspecies, two of which occur in the southeastern United States, were proposed by Staudt. Subspecies *virginiana* (including *F. australis* Rydb.), with loosely spreading trichomes on the petioles and also often on the peduncles, occurs mostly in open sites from Newfoundland westward to Alberta and southward to Georgia and Texas; it is found only infrequently on the Coastal Plain or in prairies. Plants with pinkish flowers have been distinguished as forma *maliflora* Haynie. Fernald described *F. multicipita* to include populations of the Gaspé Peninsula that have many crowns on much branched rhizomes; Reed (in Darrow, 1966) postulated that these may be virus-infected plants. Subspecies *Grayana* (Vilmorin) Staudt (*F. Grayana* Vilmorin; var. *illinoënsis* (Prince) Gray) is coarser throughout, with denser, widely spreading trichomes on the petioles and peduncles; it ranges from New York to Minnesota, south to Alabama, Louisiana, and Kansas. Subspecies *platypetala* (Rydb.) Staudt and subsp. *glauca* (Watson) Staudt occur in western North America.

The cultivated strawberry, *Fragaria* × *ananassa* Duchesne (*F. grandiflora* Ehrhart), is a hybrid between *F. virginiana* and *F. chiloënsis* that originally arose spontaneously in European gardens in the mid-18th Century; it was first recorded and illustrated by Philip Miller in 1759. The strawberry is grown commercially and in private gardens nearly throughout our area, and cultivars have persisted or escaped from cultivation in some areas. It is possible that part of the variation in *F. virginiana* may be the result of introgression with cultivated or escaped plants of *F.* × *ananassa*. In the coastal areas of Washington and British Columbia, the distributions of *F. virginiana* and *F. chiloënsis* overlap and putative natural hybrid populations occur; Staudt called these plants *F.* × *ananassa* nothomorph *cuneifolia* (Nutt. ex Howell) Staudt. Almost since its discovery, *F.* × *ananassa* has been the subject of intensive breeding and selection programs that have resulted in thousands of cultivars, practically all octoploid. Numerous strains of both parental species from throughout their native ranges have been tested for traits desirable in new cultivars. Recently, other species of *Fragaria* have been hybridized with *F.* × *ananassa* in attempts, for example, to introduce the distinctive flavors and aromas of *F. moschata* and *F. vesca* into cultivated strawberries.

Hypotheses about the relationships and evolution of the species have come from the multitudinous genetical and cytological studies and from recent chemical and intergeneric hybridization analyses. The diploid species are quite different from each other morphologically and are difficult to hybridize, with the exception of the closely related *Fragaria nubicola* and *F. viridis* Duchesne. Hybrids between diploids are usually weak and largely sterile, although meiosis is nearly regular, suggesting that the genomes are mostly homologous with merely cryptic structural or plasmatic differences. The tetraploid species are interfertile, and it has been suggested that *F. orientalis* is an autopolyploid of *F. vesca*. The hexaploid *F. moschata* has perhaps two *F. viridis* or *F. nubicola* genomes and one genome of *F. vesca*. The octoploids *F. virginiana* and *F. chiloënsis* are of complex and probable polyphyletic origins, although they can be hybridized readily. Staudt (1959) believes that the octoploids could not have been derived from the American populations of *F. vesca*, but that they share characters with eastern Asiatic diploid species such as *F. Iinumae* and *F. Daltoniana* J. Gay. Bringhurst and his associates think that *F. chiloënsis* is derived from *F. viridis* and American *F. vesca*, while *F. viridis*, *F. Iinumae*, and European and American *F. vesca* are in the genealogy of *F. virginiana*.

Bringhurst and his associates have studied extensively natural hybrid populations between *Fragaria vesca* and *F. chiloënsis* in coastal California. Numerous novel ploidy groups were observed. These, and the postulated origins of their parental gametes are: pentaploid ($2n = 35$; reduced diploid + reduced octoploid), hexaploid ($2n = 42$; unreduced diploid + reduced octoploid), enneaploid ($2n = 63$; reduced diploid + unreduced octoploid), decaploid ($2n = 70$; unreduced pentaploid + unreduced pentaploid), decaploid (reduced octoploid + unreduced hexaploid hybrid), 12-ploid ($2n = 84$; unreduced octoploid + reduced octoploid), and 14-ploid ($2n = 98$; double-unreduced pentaploid + reduced octoploid). Instances of unreduced and double-unreduced gametes in *Fragaria*, particularly in polyploid hybrids, also have been reported by several other investigators, and it is now thought that such gametes may have played a significant role in the evolution of polyploid *Fragaria* species. Although apomixis has been reported in *Fragaria*, it does not seem to have been a major evolutionary force in the genus.

The flowers of diploid species of *Fragaria* are perfect, except in *F. vesca* subsp. *bracteata*, while perfect and imperfect flowers occur in polyploid species; *F. chiloënsis* subsp. *sandwicensis* and *F. chiloënsis* f. *chiloënsis* among the polyploids have perfect flowers only. The expression of staminate or carpellate flowers is evidently the result of a single gene with multiple alleles. The allele that prevents the formation of functional stamens (abbreviated by Staudt as Su^F) is dominant over the allele that blocks the development of normal carpels (Su^M), and both these alleles are dominant over the factor for the production of perfect flowers (Su^+). In the hexaploid *F. moschata*, one Su^F takes precedence over five Su^M or Su^+ factors and one Su^M is dominant over five Su^+ factors. While such polymorphism assures a high degree of cross-fertilization in polyploid species, some outcrossing is obligatory in perfect-flowered plants, since the stigmas toward the center of the receptacle are receptive before the anthers of that flower dehisce.

At least four different intergeneric hybrids have resulted from crosses between *Fragaria* (carpellate) and *Potentilla* (staminate). A pentaploid hybrid arose from the cross *F.* × *ananassa* ($2n = 56$) × *P. fruticosa* var. *grandiflora* ($2n = 14$); a 7-ploid hybrid from *F.* × *ananassa* × *P. palustris* ($2n = 42$); a hexaploid hybrid from [*F. vesca* × *F.* × *ananassa*, $2n = 70$] × *P. fruticosa* var. *grandiflora*; and a triploid hybrid from autotetraploid *F. vesca* ($2n = 28$) × *P. fruticosa* var. *grandiflora*. Pollen of *P. anserina*, *P. anglica*, *P. erecta*, *P*, *reptans*, *P. rupestris*, and *P. nepalensis* will stimulate the production of normal fruit with large achenes on plants of *F. vesca*. A hybrid has been reported between *F. vesca* (carpellate) and *Duchesnea indica* (staminate). Knobloch (see family references) lists three hybrids between *Rubus* cultivars and an unnamed species of *Fragaria*.

Generic lines are difficult to draw in tribe Fragarieae, and arguments can be presented for the recognition of only one genus or for as many as 17. *Potentilla* is treated here in a broad sense to include *Argentina* Hill, *Comarum* L., *Pentaphylloides* Duhamel, *Dasiphora* Raf., and *Sibbaldiopsis* Rydb.; *Fragaria* L. and *Duchesnea* J. E. Sm. are maintained. Other members of this tribe are *Horkelia* Cham. & Schlecht. (17 spp. mostly of California), *Ivesia* Torrey & Gray (22 spp., western North America), *Purpusia* Brandegee (2 spp. of Nevada, Arizona, California, and Baja California), *Stellariopsis santalinoides* (Gray) Rydb. (California), *Chamaerhodos* Bunge (5 spp. of eastern Asia, especially Siberia, and northwestern North America), and *Sibbaldia* L. (a complex of 6 to 20 species of boreal, arctic, and alpine regions of the Northern Hemisphere).

REFERENCES:

A large number of references, many containing biologically important information, have had to be omitted because of limitations of space. In the following list those works that have extensive bibliographies are noted in the annotations. Consult *Horticultural Abstracts* for current horticultural references. Under subfamily references see BESSEY, BRESINSKY, RYDBERG, and SCHAEPPI & STEINDL; under family references see BATE-SMITH, CHUTE, FREE, HEGI, HULTÉN (1958), LÖVE & LÖVE, RICKETT, ROBERTSON, ROEMER & RUDORF, and ROSS-CRAIG.

AALDERS, L. E. Production of maternal-type plants through crosses to apomictic species. Nature **204**: 101, 102. 1964. [Diploid and octoploid *Fragaria* cultivars can set seed apogamously.]

ANDERSON, W. The strawberry, a world bibliography, 1920–1966. 731 pp. Metuchen, New Jersey. 1969. [An invaluable key to the literature on strawberries.]

ARNEY, S. E. Studies of growth and development in the genus *Fragaria*. I. Factors affecting the rate of leaf production in 'Royal Sovereign' strawberry. Jour. Hort. Sci. **28**: 73–84. 1953; * II. The initiation, growth, and emergence of leaf primordia in *Fragaria*. Ann. Bot. II. **17**: 477–492. 1953; III. The growth of leaves and shoot. *Ibid.* **18**: 349–365. 1954; IV. Winter growth. *Ibid.* **19**: 265–276. 1955; V. Spring growth. *Ibid.* 277–287; VI. The effect of photoperiod and temperature in leaf size. Jour. Exper. Bot. **7**: 65–79. 1956; VII. The effect of defoliation on leaf growth. Phyton Buenos Aires **5**: 93–105. 1955; VIII. The effect of defoliation on leaf initiation and early growth of the leaf initials. *Ibid.* **6**: 109–120. 1956; IX. An investigation of floral initiation under natural conditions. *Ibid.* **7**: 89–102. 1956.

ASKER, S. An intergeneric *Fragaria* × *Potentilla* hybrid. Hereditas **64**: 135–139. 1970. [*F. moschata* ♀ × *P. fruticosa* ♂.]

———. Some viewpoints on *Fragaria* × *Potentilla* intergeneric hybridization. *Ibid.* **67**: 181–190. 1971.

BEREZENKO, N. P. On studying microsporogenesis, male gametophyte and embryogenesis in *Fragaria grandiflora* Ehrh. (In Ukrainian; Russian and English summaries.) Ukrain. Bot. Zhur. **26**(4): 82–89. 1969.

BERIDZE, R. K. Phylogenetic relations and evolution of the genus *Fragaria* in the light of the new experimental data. X Int. Bot. Congr. Abstr. 332, 333. 1964.

BRINGHURST, R. S., & T. S. GILL. Unreduced and double-unreduced gametes in the evolution of polyploid *Fragaria* species. XI Int. Bot. Congr. Abstr. 22. 1969.

——— & ———. Origin of *Fragaria* polyploids. II. Unreduced and double-unreduced gametes. Am. Jour. Bot. **57**: 969–976. 1970. [For Part I, see SENANAYAKE & BRINGHURST.]

——— & D. A. KHAN. Natural pentaploid *Fragaria chiloënsis* — *F. vesca* hybrids in coastal California and their significance in polyploid *Fragaria* evolution. *Ibid.* **50**: 658–661. 1963.

———, ——— & V. VOTH. Biochemical relationships among *Fragaria* species. (Abstr.) *Ibid.* **51**: 688. 1964. [Phylogenetic relationships previously determined by cytology (see SENANAYAKE & BRINGHURST) confirmed.]

——— & Y. D. A. SENANAYAKE. The evolutionary significance of natural *Fragaria chiloënsis* × *F. vesca* hybrids resulting from unreduced gametes. *Ibid.* **53**: 1000–1006. 1966.

———, ——— & D. A. KHAN. *Fragaria* polyploids, chromatographic analysis. (Abstr.) *Ibid.* **53**: 638. 1966. [Relationships of 9 species.]

BROWN, T., & P. F. WAREING. The genetical control of the everbearing habit and three other characters in varieties of *Fragaria vesca*. Euphytica **14**: 97–112. 1965. [Also runner production and fruit color.]

BUMAGINA, S. I., & E. MESAROSH. The evaluation of the results of interspecific hybridization in strawberry species *Fragaria vesca* L., *Fragaria viridis* Duch., *Fragaria moschata* Duch. based on the seed formation set in the hybrids and on the viability of the hybrid seeds. (In Russian; English summary.) Genetika Moscow **5**(5): 32–38. 1969.

COMSTOCK, R. E., T. KELLEHER, & E. B. MORROW. Genetic variation in an asexual species, the garden strawberry. Genetics **43**: 634–646. 1958.

DAHLGREN, K. V. O. Die Lösung des *micrantha*-Problems bei *Fragaria vesca*. (English summary.) Bot. Not. **115**: 288–292. 1962. [The *micrantha* characters are the result of a periclinal chimera.]

DARROW, G. M. The strawberry: history, breeding and physiology. xiv + 447 pp. *frontisp. 52 col. pls.* New York. 1966. [A useful, up-to-date book that covers many topics; extensive references.]

DOGADKINA, N. A. A contribution to the question of genome relations in some species of *Fragaria*. Compt. Rend. Acad. Sci. URSS II. **30**: 166–168. 1941. [*F. vesca* × *F.* × *ananassa; F. orientalis* × *F. moschata.*]

Duchesne, A. N. Histoire naturelle des fraisiers, xii + 324 pp. Chart + 118 pp. (Remarques particulières.) Paris. 1766. [A remarkable work that still is the basis for modern studies; see Guédès.]

———. Fraisier, *Fragaria*. *In*: J. B. Lamarck, Encycl. Méthod. Bot. **2**: 527–540. 1788.

Ellis, J. R. The allopolyploid hybrid between *Fragaria vesca* and *F. moschata*. (Abstr.) Proc. XI Int. Congr. Genet. **1**: 209, 210. 1963.

———. Cytogenetic studies in the genera *Fragaria* and *Potentilla*. Ph.D. Thesis. Univ. Manchester. 263 pp. 1958.*

———. *Fragaria-Potentilla* intergeneric hybridization and evolution in *Fragaria*. Proc. Linn. Soc. London **173**: 99–106. *pls. 1, 2.* 1962.

Evans, W. D., & J. K. Jones. Incompatibility in *Fragaria*. Canad. Jour. Genet. Cytol. **9**: 831–836. 1967. [*F. vesca, F. viridis, F. nubicola, F. nilgerrensis.*]

Fadeeva, T. S. Problems of comparative plant genetics. 1. Principles of the genome analysis on the example of the genus *Fragaria*. Genetika Moscow **1966**(1): 12–28. 1966; 2. Genetics of characters and mutations in the strawberry. *Ibid.* **1966**(7): 100–117. 1966; 3. The study of intraspecific variability of the natural species forms in *Fragaria vesca* L. Vestn. Leningrad. Univ. **1966**(21): 126–135. 1966; 4. The potential of genetic variability of species as exemplified by the genus *Fragaria*. Genetika Moscow **1966**(12): 36–45. 1966. [All articles in Russian with English summaries.]

——— & A. I. Dyatlova. Dynamics of germination of achenes of the reciprocal hybrids of strawberry. (In Russian.) Bot. Zhur. **47**: 1190–1194. 1962.

——— & V. N. Migalovskaya. Cytogenetical study of hybrids between three species in the genus *Fragaria* L. (In Russian; English summary.) Vestn. Leningrad. Univ. **1966**(2): 119–131. 1966. [*F. vesca, F. viridis, F. moschata.*]

Federova, N. J. Crossability and phylogenetic relations in the main European species of *Fragaria*. Compt. Rend. Acad. Sci. URSS II. **52**: 545–547. 1946.

Gupta, B. K. Chromosome survey in strawberries of Kashmir. Cytologia **35**: 107–110. 1970.

Guédès, M. Notules de bibliographie botanique V — VIII. Jour. Soc. Bibliogr. Nat. Hist. **6**: 174–180. 1972. [VII. Un exemplaire de l'essai sur l'histoire naturelle des fraisiers de Duchesne annoté par l'auteur, 177.]

Guttridge, C. G. Evidence for a flower inhibitor and vegetative growth promoter in the strawberry. Ann. Bot. II. **23**: 351–360. 1959. [See also *ibid.* 612–621.]

Haskell, G., & H. Williams. Biometrical variation in flowers of a polyploid series of strawberries. Jour. Genet. **52**: 620–630. 1954. [Diploid, hexaploid, and octoploid spp.; cultivars.]

Hedrick, U. P., *ed.* Sturtevant's notes on edible plants. vii + 686 pp. *frontisp.* Vol. 2(2), 27th Annual Rep. N.Y. State Agr. Exper. Sta. Albany. 1919. [*Fragaria*, 273–282; includes discussion on the strawberry in classical and pre-Linnaean literature; also see Sturtevant, Trans. Mass. Hort. Soc. **1888**: 191–204. 1888.]

Hylander, N. Linnaeus, Duchesne and the strawberries. Sv. Linné-Sällsk. Årsskr. **28**: 17–40. 1945. [Reviews correspondence between Linnaeus and Duchesne; in Swedish with English summary on pp. 95, 96.]

ISLAM, A. S. Possible role of unreduced gametes in the origin of polyploid *Fragaria*. Biologia Lahore **6**: 189–192. 1960.

———. Reinvestigation into the reported instances of paternal and maternal inheritance in *Fragaria*. *Ibid*. 241–251. [Includes mention of a haploid *F. vesca* derived by parthenogenesis from a cross between a diploid *F. vesca* and an octoploid.]

JAHN, O. L., & M. N. DANA. Crown and inflorescence development in the strawberry, *Fragaria ananassa*. Am. Jour. Bot. **57**: 606–612. 1970.

——— & ———. Effects of cultivar and plant age on vegetative growth of the strawberry, *Fragaria ananassa*. *Ibid*. 993–999.

JONES, J. K. Cytogenetical studies in genera *Fragaria* and *Potentilla*. Ph.D. Thesis, Univ. Manchester. 1955.*

KALKMAN, C. *Potentilla*, *Duchesnea*, and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968. [Notes on generic delimitation.]

KAHN, D. A. Cytogenetics and inheritance of certain morphological and biochemical characters in *Fragaria* hybrids involving species of different ploidy levels. 151 pp. Ph.D. Thesis, Univ. California, Davis. 1964.* [Diss. Abstr. **26**(4): 1873B. 1965.]

KLIMSTRA, W. D., & F. NEWSOME. Some observations on the food coactions of the common box turtle, *Terrapene c. carolinae*. Ecology **41**: 637–647. 1960. [*Fragaria* fruits eaten.]

LEBEGUE, A. Recherches sur la polyembryonie chez les Rosacées (g. *Fragaria* et *Alchemilla*). Bull. Soc. Bot. France **99**: 273–275. 1952. [*F. vesca*.]

LOSINA-LOSINSKAJA, A. S. Révision critique du genre *Fragaria*. (In Russian; Latin diagnoses; French résumé.) Izv. Glavn. Bot. Sada SSSR **25**: 47–88. 1926.

MCFADDEN, W. H., R. TERANISHI, J. CORSE, D. R. BLACK, & T. R. MON. Volatives from strawberries. II. Combined mass spectrometry and gas chromatography on complex mixtures. Jour. Chromatography **18**: 10–19. 1965. [Over 150 components found, most of them identified.]

NÜRNBERG-KRÜGER, U. Genetische Untersuchungen an diploiden *Fragaria*-Arten. I. Die Kreuzung zwischen *Fr. vesca* und *Fr. nilgerrensis*, ihre Auswirkung auf die Morphologie der Pflanzen und die Ausbildung des Geschlechts. Zeitschr. Vererbungslehre **89**: 747–773. 1958.

SATTLER, R. Organogenesis of flowers. xxvi + 207 pp. Toronto. 1973. [*F. vesca*, 72–77; excellent photographs of floral development.]

SENANAYAKE, Y. D. A. Morphological, cytological and biochemical studies on *Fragaria* interspecific hybrids and on *Fragaria-Potentilla* intergeneric hybrids. 179 pp. Ph.D. Thesis, Univ. California Davis. 1966.* [Diss. Abstr. **27**: 698B. 1966.]

———& R. S. BRINGHURST. Origin of *Fragaria* polyploids. I. Cytological analysis. Am. Jour. Bot. **54**: 221–228. 1967.

SMEETS, L. Runner formation on strawberry plants in autumn and winter. I. Euphytica **4**: 53–59. 1955; II. Influence of the light intensity on the photoperiodic behavior. *Ibid*. 240–244.

———. Influence of the temperature on runner production in five strawberry varieties. *Ibid*. **5**: 13–17. 1956.

SONDHEIMER, E., & C. B. KARASH. The major anthocyanin pigments of the wild strawberry (*Fragaria* vesca). Nature **178**: 648, 649. 1956.

SOUÈGES, R. Observations embryologiques sur quelques *Fragaria* de culture. Bull. Soc. Bot. France **82**: 458–461. 1935.

STAUDT, G. Über Fragen der phylogenetischen Entwicklung einiger Arten der Gattung *Fragaria*. Züchter **21**: 222–232. 1951. [Includes distribution maps of the spp.]

———. Cytogenetische Untersuchungen an *Fragaria orientalis* Los. und ihre Bedeutung für Artbildung und Geschlechts-differenzierung in der Gattung *Fragaria* L. Zeitschr. Indukt. Abst. Vererbungslehre **84**: 361–416. 1952.

———. Die geographische Verbreitung der Gattung *Fragaria* und die Bedeutung für die Phylogenie der Gattung. Ber. Deutsch. Bot. Ges. **66**: 236–238. 1953.

———. Die Vererbung des Geschlechts beider tetraploiden, diözischen *Fragaria orientalis* Los. *Ibid*. **67**: 384–387. 1954.

———. Cytotaxonomy and phylogenetic relationships in the genus *Fragaria*. (Abstr.) Proc. IX Int. Bot. Congr. **2**: 377. 1959.

———. Die Entstehung und Geschichte der grossfrüchtigen Gartenerdbeeren *Fragaria* × *ananassa* Duch. Züchter **31**: 212–218. 1961.

———. Taxonomic studies in the genus *Fragaria*; typification of *Fragaria* species known at the time of Linnaeus. Canad. Jour. Bot. **40**: 869–886. *pls. 1, 2.* 1962. [The best modern survey of the genus, although it is difficult to ascertain Staudt's delimitation of New World subspecific taxa since descriptions and synonyms are not given.]

———. Die Genetik und Evolution der Heterözie in der Gattung *Fragaria*. I. Untersuchungen an *Fragaria orientalis*. Zeitschr. Pflanzenz. **58**: 245–277. 1967; II. Die Artkreuzungen *F. vesca* × *F. orientalis* und *F. viridis* × *F. orientalis*. *Ibid*. 309–322; III. Untersuchungen an hexa- und oktoploiden Arten. *Ibid*. **59**: 83–102. 1968. [All with English summaries.]

———. Tests for apomixis in strawberries. Hort. Res. Edinburgh **10**(2): 148–150. 1970.*

———. *Fragaria iturupensis*, eine neue Erdbeerart aus Ostasien. Willdenowia **7**: 101–104. 1973. [The only octoploid known from outside the New World.]

THOMPSON, P. A. The development of embryo, endosperm, and nucellus tissues in relation to receptacle growth in the strawberry. Ann. Bot. II. **27**: 589–605. *pl. 1.* 1963.

WATKINS, R., & L. P. S. SPANGELO. Components of genetic variance in the cultivated strawberry. Genetics **59**: 93–103. 1968.

———, ——— & A. T. BOLTON. Genetic variance components in cultivated strawberry. Canad. Jour. Genet. Cytol. **12**: 52–59. 1970.

WESTERGAARD, M. The mechanism of sex determination in dioecious flowering plants. Adv. Genet. **9**: 217–281. 1958. [*Fragaria*, 232–235.]

WINTER, M., & B. WILLHALM. Sur l'arôme des fraises fraîches. Analyse des composés carbonylés, esters et alcools volatils. Helvet. Chim. Acta **47**: 1215–1227. 1964.

10. **Duchesnea** J. E. Smith, Trans. Linn. Soc. London 10: 372. 1811.

Herbaceous perennials with rosettes of leaves on short, vertical rootstocks and long, prostrate, leafy, sympodially branching stems; adventitious plants produced frequently at nodes along the prostrate stems. Leaves radical and cauline, trifoliolate (infrequently simple), long petiolate; leaflets nearly equal in size, serrate at least in the upper parts, short petiolulate; stipules of the rosette leaves adnate for half their length to the petiole, those of the cauline leaves ± free. Inflorescences 1-flowered, arising from the rosettes and also axillary along the prostrate stems; evidently ebracteate. Flowers perfect, borne on long pedicels. Calyx lobes 5, equaling or exceeding the petals, valvate in aestivation, entire, narrowly triangular, alternate with the 5 obovate, apically 3–5-toothed epicalyx lobes, both epicalyx and calyx lobes enlarging with the fruit and becoming reflexed; floral cup short, saucer-shaped, free of the carpels, a nectar ring scarcely evident. Petals 5, yellow, spreading, deciduous, narrowly obovate with ± entire margins, inserted at edge of floral cup, imbricate. Androecium of 15–25 stamens in multiples of 5, some persistent; filaments of 3 lengths, free, perigynous at edge of floral cup; anthers yellow. Gynoecium of many free carpels on an elevated, ± hemispheric receptacle that enlarges in fruit; styles inserted adaxially above the middle of the carpels, promptly caducous; stigmas terminal, discoid; each carpel with one pendulous and anatropous ovule, the micropyle superior. Accrescent receptacle red, much like that of *Fragaria*, subcarnose, neither aromatic nor flavorful, subtended by the persistent calyx and epicalyx, the entire fruits sometimes falling from the plants. Achenes red, numerous, minute, superficial, with an adaxial appendage, falling from the enlarged receptacle; embryo filling the achene, the radicle superior, slightly bent. Base chromosome number 7. (Not *Duchnesia* Cass., 1817). TYPE SPECIES: *D. fragiformis* J. E. Sm., nom. illegit. = *D. indica* (Andrews) Focke. (In commemoration of Antoine Nicolas Duchesne, 1747–1827, author of an early, quite remarkable monograph on *Fragaria*.) — INDIAN STRAWBERRY.

Probably two species of the Old World, with *Duchesnea indica* (*Fragaria indica* Andrews; *Potentilla indica* (Andrews) Wolf), $2n = 84$, indigenous from Afghanistan and India to China, Laos, Vietnam, Korea, Japan, Taiwan, and the Philippine Islands (introduced into Malesia, Europe, and the New World), and *D. chrysantha* (Zoll. & Moritzi) Miquel, $2n = 14$, 28?, ranging from Japan to southern China, India, Taiwan, the Philippines, Sumatra, and Java.

Duchesnea indica is naturalized, mostly in open areas such as waste ground, lawns, roadsides, and pastures, in the eastern United States from northern Florida westward to eastern Texas and northward to southern Connecticut and New York, Ohio, Indiana, Illinois, Iowa, Arkansas, and Oklahoma; it is also found occasionally on the Pacific Coast, primarily east of the Cascade Mountains. This species is cultivated as a ground cover or basket plant or as a low climber.

Plants of *Duchesnea indica* and *D. chrysantha* have a great resemblance, particularly when in fruit, to *Fragaria* species and are sometimes included within that genus. However, this similarity is probably the result of parallel evolution. *Duchesnea* is perhaps more closely related to *Potentilla*, and both Wolf (cf. *Potentilla*) and Kalkman alluded to affinities with *P. reptans*. Artificial intergeneric hybrids are *D. indica* × *P. reptans* and *F. vesca* × *D. indica*. The F_1 hybrids of the first cross are quite vigorous and produce numerous flowers but no fruit, while those of the second cross are weak and do not flower.

The achenes of *Duchesnea indica* sometimes have an adaxial appendage similar to the elaiosomes of *Potentilla* sect. FRAGARIASTRUM; the function of such appendages in *Duchesnea* is not known, but in *Potentilla* sect. FRAGARIASTRUM they evidently aid in the distribution of the achenes by ants. It has been reported that birds may eat the fruits of *D. indica*.

REFERENCES:

Under subfamily references see RYDBERG; under family references see BATE-SMITH, BUNTING, CHUTE, RICKETT.

ANDREWS, H. *Fragaria indica*, Indian strawberry. Bot. Repos. **7**: *pl. 479*. 1807.

HARA, H., & S. KUROSAWA. On the *Duchesnea indica* group. Jour. Jap. Bot. **34**: 161–166. 1959. [The only modern world-wide taxonomic revision.]

HASKELL, G., & H. WILLIAMS. Biometrical variation in flowers of a polyploid series of strawberries. Jour. Genet. **52**: 620–630. 1954. [Includes *D. indica*.]

HSU, C. C. Preliminary chromosome studies on the vascular plants of Taiwan (II). Taiwania **14**: 11–27. 1968. [*D. chrysantha*, $2n = 28$.]

KALKMAN, C. *Potentilla*, *Duchesnea*, and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968. [Notes on generic delimitation; *D. indica* placed in *Potentilla*.]

KER-GAWLER, J. B. *Fragaria indica*. Yellow-flowered strawberry. Bot. Regist. **1**: *pl. 61*. 1815.

MANGELSDORF, A. J., & E. M. EAST. Studies on the genetics of *Fragaria*. Genetics **12**: 307–339. 1927. [Includes mention of a hybrid between *D. indica* and *F. vesca*.]

WIGHT, R. G. *Fragaria indica*. Ic. Pl. Indiae Orient. **3**: *pl. 989*. 1845.

11. **Potentilla** Linnaeus, Sp. Pl. 1: 495. 1753; Gen. Pl. ed. 5. 219. 1754.

Perennial or infrequently annual or biennial herbs, rarely shrubs, often with long rhizomes covered with persistent leaf bases, the plants rosulate, caespitose, or with creeping stems rooting at nodes, sometimes with true stolons. Leaves basal and/or cauline, digitate, trifoliolate, or imparipinnate, the lower leaves long petiolate; leaflets toothed to dissected, sessile or shortly petiolulate; stipules of the basal leaves adnate for most of their length to the petioles and forming membranaceous wings, those of the cauline leaves mostly free, entire, linear or deeply parted. Inflorescences lax cymes or single flowered, arising from the crowns and/or creeping stems, long pedunculate; bracts often foliaceous, deeply divided. Flowers pale to bright yellow or white [or reddish-purple], usually perfect. Calyx with an epicalyx, the epicalyx lobes 5 (4), alternate with and usually equaling, but narrower than, the 5 (4) calyx lobes, both spreading at anthesis, valvate in aestivation; floral cup saucer-shaped or hemispheric, free of the carpels, a nectar ring often prominent. Petals 5 (4), spreading, deciduous, imbricate, orbicular, obovate, or cuneate, the apices often emarginate, the bases rounded, seldom clawed, inserted at the edge of the floral cup. Androecium of 10–30, usually 20, stamens, infrequently fewer or more, sometimes in fascicles; filaments tapering-filiform, free to the base, perigynous at the inside margin of the nectar ring; anthers yellow, basifixed,

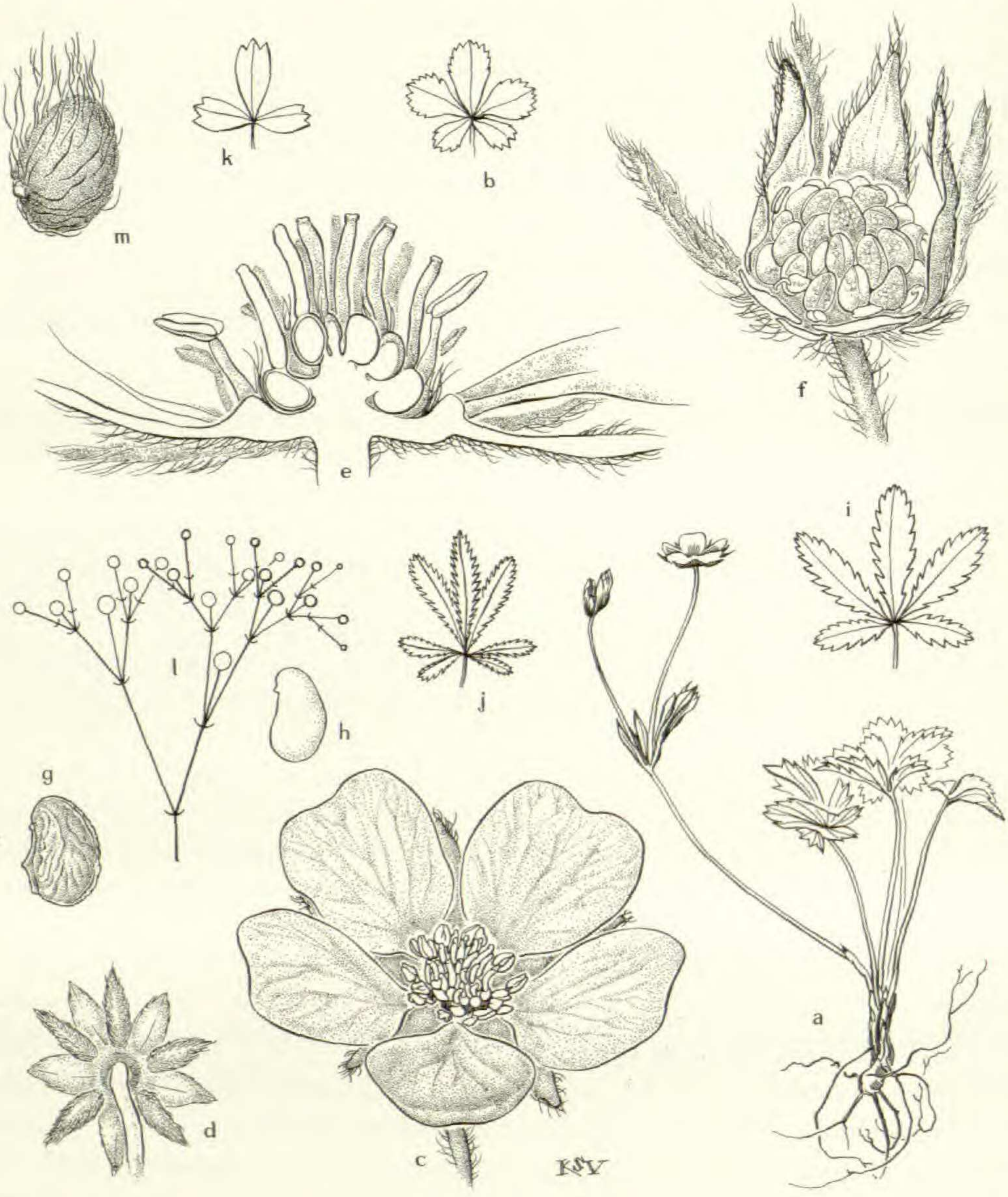

FIGURE 7. **Potentilla.** a–h, *P. canadensis*: a, young plant with first flowers of season, × 1; b, basal leaf, × 1/2; c, flower, × 5; d, lower side of flower showing epicalyx and calyx lobes, petals not shown, × 3; e, vertical section of flower, petals inserted at the edge of floral cup, stamens inserted at inside margin of nectar ring, carpels on a hemispherical receptacle, × 12; f, fruit, 2 epicalyx and 2 calyx lobes removed, × 3; g, achene, × 12; h, seed, × 12. i, *P. simplex*: leaf, × 1/2. j, *P. recta*: leaf, × 1/4. k–m, *P. tridentata*: k, leaf, × 1/2; l, diagrammatic sketch of inflorescence, × 1/2; m, achene, × 12.

didymous. Gynoecium of many [rarely only 5 or 10] simple, free carpels on a hemispherical or conical receptacle; style terminal or lateral to nearly basal on the adaxial side of the carpel, basally articulated, deciduous, filiform or short and basally thickened; stigma terminal, discoid; each carpel with a single, anatropous and pendulous, ascending, or descending ovule, the micropyle adaxial or abaxial. Accessory fruits dry, surrounded or inclosed by the persistent, often accrescent calyx, the receptacle seldom enlarging. Achenes smooth or variously textured, pubescent or not, sometimes appendaged, at maturity detaching from the receptacle; embryo filling the achene, the radicle inferior or superior. Base chromosome number 7. (Including *Argentina* Hill, *Comarum* L., *Dasiphora* Raf., and *Drymocallis* Fourreau ex Rydb.) LECTOTYPE SPECIES: *P. reptans* L., see P. A. Rydberg, N. Am. Fl. 27: 293. 1908. (Name the diminutive of Latin *potens*, powerful; originally applied to *P. anserina* for its reputed medicinal powers.) — CINQUEFOIL, FIVE-FINGER.

A taxonomically complex genus of perhaps 300 species of the North Temperate Zone. The frequent occurrence of polyploidy, hybridization, apomixis, and ecotype formation makes the number of biological species impossible to determine at present. The genus is most diverse in northern Eurasia, and many species are of arctic or montane regions. Not many species are common to both the Eastern and Western hemispheres, and there are very few indigenous species south of the equator. In North America, the genus is particularly well developed in the western Cordillera. Eleven species (four introduced from Europe) representing three infrageneric categories occur in our area.

The classification of the genus is based largely on the treatments of the North American species by Rydberg (1898, 1908), who divided *Potentilla*, sensu lato, into several segregate genera (with his restricted *Potentilla* including 176 species in 31 groups of undesignated rank), and the worldwide revision of Wolf (1908) who assigned the 305 recognized species to 2 sections, 6 subsections, and 31 greges. (Citations of infrageneric categories need to be checked carefully, since many names are not validly published, several nonhomologous systems of classification have been used, and many ranks are incorrectly given.) The numerous biosystematic investigations since 1908 show clearly that these basic classifications need extensive reconstruction before true intrageneric relationships can be reflected.

Subgenus POTENTILLA is represented in our area by nine species in two "groups." *Potentilla simplex* Michx. (*P. canadensis* auct., non L.; *P. caroliniana* Poiret) and *P. canadensis* L. (*P. pumila* Poiret; *P. caroliniana* auct., non Poiret) belong to the "Tomentillae." Both of these native species are perennial herbs with arching, nodally rooting stems that arise from basal rosettes, digitate leaves, solitary flowers, glabrous carpels (although the receptacle may be pubescent), and obliquely terminal, slender styles. Their chromosome numbers are unknown. In *P. simplex*, the rhizome is elongated and irregularly enlarged, the cauline leaves are well expanded when the flowers in their axils are at anthesis, the leaflets of mature leaves are usually less than half as wide as long and toothed nearly to the bases, and the first flower of the season is usually produced in the axil of the second fully developed cauline leaf. This species occurs in dry moist pastures, fields, thickets, open woodlands, and lawns from Newfoundland, Nova Scotia, and southern Ontario to Minnesota southward to Georgia, Louisiana, Oklahoma, and Texas. The plants characteristically have spreading-strigose stems, petioles, and peduncles. Nearly glabrous individuals have been separated as var. *calvescens* Fern. (from the northern limits of the species to South Carolina, Illinois, Missouri, and Oklahoma), while plants with the leaves silvery-sericeous beneath may be called var. *argyrisma* Fern. (Pennsylvania and Indiana to Tennessee, Illinois, Missouri, Kansas, and Arkansas). *Potentilla canadensis* differs in that the rhizome is shorter and thicker than in *P. simplex*, the cauline leaves are only partly expanded at anthesis, the leaflets of mature leaves are usually more than half as wide as long and toothed only in the upper half, and the first flower of the season is usually produced in the axil of the first fully developed cauline leaf. This species ranges from western Nova Scotia and southern Maine to southwestern Ontario and northern Ohio southward to Georgia, Alabama, and southeastern Missouri and is found mostly in dry habitats such as rocky open woods, borders, pastures, fields, and lawns. Two varieties are sometimes recognized: var. *canadensis* with the petioles, stems, peduncles, lower leaf surfaces, and calyces silky-pilose with appressed or loosely ascending, soft trichomes (from the northern limits of the species to Long Island, South Carolina, and Ohio), and var. *villosissima* Fern. with long villous, loosely spreading to reflexed indumentum (Maryland and Ohio to the southern limits of the species); Steyermark notes that the latter variety occurs on acidic soils in Missouri.

Species of the "Supinae" group (including the "Rivales," "Argenteae," and "Rectae" of Rydberg and Wolf) are annual to perennial herbs with cymose, many-flowered, leafy inflorescences terminating mostly unbranched stems that arise from the rosettes; pale to light yellow flowers; glabrous carpels; and subterminal, basally thickened styles. This group is primarily of western North America and Europe; two indigenous, one possibly circumpolar, and four introduced species occur with us. The European *Potentilla argentea* is readily recognized by the digitate leaves with narrow, deeply toothed, revolute leaflets that are densely white-tomentose beneath. Plants are usually diploid and commonly reproduce apogamously. In North America it is naturalized from Newfoundland to Washington southward to North Carolina, Tennessee, Ohio, Indiana, and Illinois. *Potentilla recta* L. (including *P. sulphurea* Lam.), erect, hirsute perennial herbs with nearly leafless cymes standing above the principal foliage; characteristic digitate leaves with 5 to 7 oblanceolate, deltoid-toothed leaflets; petals that much exceed the calyx lobes; and 30 stamens, is naturalized from Europe in grassy or ruderal areas from Newfoundland, Quebec, Ontario, and Minnesota to Georgia, Alabama, and Texas, as well as in Washington and Montana. This species shows much less variation in North America than in Europe. The only species of the "Supinae' in our area with pinnate leaves and a large, wedge-shaped appendage on the adaxial side of the achene is *P. paradoxa* Nuttall ex Torrey & Gray, which is most abundant in the Mississippi River valley, but ranges from Ontario to British Columbia southward to Pennsylvania, Ohio, Illinois, Missouri, Kansas, Louisiana, Texas, New Mexico, and northern Mexico; it evidently occurs also in eastern Asia. Allied species are *P. Nicolletii* (S. Watson) E. Sheldon of the midwestern United States (often included within *P. paradoxa*) and *P. supina* L., of Europe.

Potentilla pentandra Engelm. is a variable species with digitately quinate or ternate basal leaves (the lower leaflets deeply divided), 5 stamens, and smooth achenes. It is a plant mostly of sandy bottomlands and prairies from Minnesota to Alberta, southward to Arkansas, Kansas, and Oklahoma. The closely related *P. millegrana* Engelm. differs in the ternate leaves, petals much shorter than the calyx lobes, and 10 or 15 stamens. Not yet reported from our area, this species could occur in Arkansas, since its known range is from Manitoba and Washington to Illinois, southern Missouri, Kansas, Oklahoma, New Mexico, and California. Both *P. pentandra* and *P. millegrana* are frequently merged with *P. rivalis* Nutt. ex Torrey & Gray either at the varietal level or without taxonomic recognition; these taxa may represent an apomictic complex.

Potentilla norvegica L. (*P. monspeliensis* L.), $2n = 70$ (42, 56), is widespread in the Northern Hemisphere, occurring in North America from Greenland and Labrador to Alaska, southward to Georgia, Alabama, California, and northern Mexico; it is uncertain whether this species is indigenous to the New World. The lower leaves are digitate, with three elliptic to broadly elliptic leaflets; the calyx is accrescent in fruit; there are usually 15 or 20 stamens; and the achenes are prominently ribbed. Swedish plants of this species reproduce primarily by apomixis, which is assumed to be the common method of reproduction throughout its range. The European *Potentilla intermedia* L., $2n = 56$, which differs from *P. norvegica* by the mostly digitately basal leaves, has become naturalized from Newfoundland, Quebec, and Michigan, southward to Virginia and North Carolina. Apparently an obligate apomict, *P. intermedia* has morphological features of both *P. norvegica* and *P. argentea*, and, consequently, is thought to be of hybrid origin, although this remains to be proven. *Potentilla inclinata* Vill. (*P. canescens* Bess.) is much like the two preceding taxa, but the leaves are more densely pubescent, and the petals noticeably exceed the calyx lobes. Indigenous to Europe, *P. inclinata* may be of hybrid origin (*P. recta* × *P. argentea*); in North America it occurs from southwestern Quebec and Ontario to North Carolina, Indiana, and Michigan.

Potentilla anserina L. (*Argentina anserina* (L.) Rydb.) has been reported recently from Sevier County, Tennessee (Roger & Bosers, Castanea **34**: 395. 1969). Characterized by pinnate leaves with numerous leaflets, solitary flowers axillary along elongated stolons, glabrous carpels, and lateral, filiform styles, this species is one of the most widely distributed members of the genus, occurring from the arctic regions of North America, Europe, and Asia, to California, New Mexico, the Mediterranean area, and southeastern Asia. It occurs also in western South America from central Chile to Patagonia, and it is naturalized in Australia, Tasmania, and New Zealand. Plants from most of the eastern United States belong to subsp. *anserina* (lower leaflets silvery-sericeous beneath with straight trichomes; achenes dorsally grooved; bractlets usually toothed or lobed), $2n = 28$, 42, a variable, self-incompatible subspecies found in most parts of temperate Eurasia and North America. In the eastern United States and Europe, subsp. *anserina* grows mostly in disturbed sites, where it is often a troublesome weed, while, in the western United States, it is rarely seen except in natural, unspoiled habitats. *Potentilla anserina*, sensu lato, has been variously treated taxonomically; Rydberg divided the North American representatives into 8 species, placing them in the segregate genus *Argentina* Lam. *Potentilla anserina* is the only species of Rosaceae known to produce the trihydroxyflavonoids myricetin and leucodelphinidin, compounds that are also known from the Chrysobalanaceae.

The apomictic *Potentilla arguta* Pursh, $2n = 14$, (plant erect, glandular-villous; petals whitish; leaves pinnate; stamens 25 to 30, in 5 festoons on a thick, glandular disc; style subbasal; receptacle distinctly enlarging in fruit), was reported from the vicinity of Nashville, Tennessee, by Gattinger (Fl. Tennessee, 1901), but evidently has not been seen again in our area. Its range is from New Brunswick and Quebec to Mackenzie and British Columbia, southward to the District of Columbia, West Virginia, Ohio, Indiana, Illinois, Missouri, Oklahoma, Colorado, and Arizona. It has been placed in the segregate genus *Drymocallis* Fourr. (as *D. agrimonioides* (Pursh) Rydb.) along with related species of Eurasia and western North America, including *P. glandulosa* Lindley, one of the best studied flowering plants of North America in terms of experimental taxonomy (Clausen, Keck, & Hiesey).

Gattinger also reported *Potentilla fruticosa* L., shrubby cinquefoil, golden-hardhack, of subg. TRICHOTHALAMUS (Lehm.) Reichenb. (shrubs with pinnate leaves, the leaflets entire; style clavate, subbasal; carpels pubescent) from Cherokee County, North Carolina. Elkington recognized two subspecies: subsp. *fruticosa* (tetraploid; plants dioecious) that ranges from Ireland and northern Europe to Asia, and subsp. *floribunda* (Pursh) Elkington (diploid; flowers perfect) that occurs in southern Europe, Turkey, the Caucasus Mountains, Asia to Japan and the Kamchatkan Peninsula, and North America from Labrador to Alaska southward to Pennsylvania, Ohio, Indiana, Illinois, Iowa, South Dakota, Arizona, New Mexico, and California. The other species of subg. TRICHOTHALAMUS are from eastern Asia. This group has been treated at the generic level as *Dasiphora* Raf. or *Pentaphylloides* Duhamel.

Potentilla tridentata Aiton (*Sibbaldiopsis tridentata* (Aiton) Rydb., $2n = 28$, three-toothed cinquefoil, of subg. SIBBALDIOPSIS (Rydb.) Boivin, a low perennial with creeping, woody stems from a caudex; ternately compound leaves with evergreen, coriaceous, apically 3- or 5-toothed leaflets; white petals; filiform, basal styles; and pubescent carpels is primarily of subarctic regions, occurring from Greenland, Labrador, and Mackenzie to New England, New York, Michigan, Wisconsin, Iowa, and North Dakota, and southward in scattered localities in the Appalachian Mountains to northern Georgia. *Potentilla ambigua* Camb., of the Himalayas, and *P. Miyabei* Makino, of Japan, are possibly close relatives.

Several types of breeding systems occur in *Potentilla*. Some species are diploid (*P. fruticosa* subsp. *floribunda*) or polyploid (*P. anserina, P. recta, P. tridentata*) and sexually reproducing, often with extensive ecotype formation; others are apomictic diploids (*P. argentea, P. arguta*), a situation very rare among the flowering plants; and many are part of polyploid-agamic complexes (*P. canescens, P. intermedia, P. norvegica*). The type of reproduction, and often even the chromosome number, is not known for most of the common species indigenous to eastern North America (e.g., *P. canadensis, P. paradoxa, P. pentandra, P. rivalis*, and *P. simplex*). Apomixis occurs most commonly in sect. GYMNOCARPAE subsects. *Conostylae* and *Gomphostylae*, of Wolf. Unreduced embryo sacs of apomictic *Potentilla* species usually are produced aposporously, although both diospory and diplospory occur in the British *P. Tabernaemontani.* Since the archesporangium is multicellular, the distinction between the two types of embryo sac development is difficult to determine and may not be indicative of any fundamental difference in *Potentilla.* The apomicts are pseudogamous, and fertilization of the polar nuclei is necessary for seed development; pollen of even distantly related species often functions, although seed set is reduced. All transitions occur between complete sexuality, facultative apomixis, and obligate apomixis. Even in the last case, unreduced egg cells can occasionally be fertilized. Throughout the genus, aneuploidy and odd-level polyploids are very rare; chromosome numbers range from $2n = 14$ to 112; no triploid apomicts are known from nature. The genetic control of apomixis is still poorly known but is believed to involve several genes. Asker (1966, 1970–71) has shown that sexual tetraploids resulted from colchicine treatment of apomictic diploids, and he also has evidence that polyploidization and hybridization between apomicts may interfere with the production of unreduced embryo sacs. "In *Potentilla,* facultative apomicts may have arisen on the diploid level, later giving rise to polyploids with stabilized obligate apospory; but . . . an independent origin of apomixis in polyploids is also possible, at least where the *argentea* complex is concerned" (Asker, 1970–71, III).

REFERENCES:

Under subfamily references see BESSEY, BRESINSKY, NESTLER, RYDBERG, and SCHAEPPI & STEINDL; under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHUTE, DEVADAS & BECK, DIPPLE, GUSTAFSSON, HARA, HEGI, HULTÉN (1958, 1971), JESSON, LUBBOCK, REHDER, RICKETT, ROBERTSON, ROSS-CRAIG, SCHNEIDER, and VINES.

ASKER, S. Induced sexuality after chromosome doubling in an apomictic *Potentilla argentea*-biotype. Hereditas **57**: 339–342. 1967.

———. Apomictic biotypes in *Potentilla intermedia* and *P. norvegica. Ibid.* **66**: 101–108. 1970.

———. Apomixis and sexuality in the *Potentilla argentea* complex. I. Crosses with other species. *Ibid.* 127–144. II. Crosses within the complex. *Ibid.* 189–204. III. Euploid and aneuploid derivatives (including trisomics) of some apomictic biotypes. *Ibid.* **67**: 111–142. 1971.

———. Some viewpoints on *Fragaria* × *Potentilla* intergeneric hybridization. *Ibid.* 181–190. [Good review paper.]

———. Studies in apomictic and sexual *Potentilla* L. 7 pp. Lund, Sweden. 1971.

[Abstract of papers submitted as a doctoral thesis to the University of Lund.]

——— J. & S. FRÖST. Chromatographic studies in *Potentilla argentea* L. Hereditas **62**: 426–429. 1969.

——— & ———. Chromatographic studies of phenolic compounds in apomictic *Potentilla* L. *Ibid.* **65**: 241–250. 1970.

——— & ———. Plant age and chromatographic pattern in *Potentilla. Ibid.* **72**: 149–152. 1972. [*P. argentea, P. canescens, P. norvegica.*]

BORHIDI, A., & I. ISÉPY. Statistical studies on *Potentilla* species. Acta Bot. Acad. Sci. Hungar. **12**: 221–239. 1966.*

BOWDEN, W. M. Cytotaxonomy of *Potentilla fruticosa*, allied species and cultivars. Jour. Arnold Arb. **38**: 381–388. 1957.

CARLBLOM, C. Premeiotic reduction in *Agrostis* L., *Potentilla* L. and *Triticum* L. Hereditas **61**: 421–423. 1969. [*P. argentea.*]

CLAUSEN, J., D. D. KECK, & W. M. HIESEY. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Publ. **520**: vii + 452 pp. 1940. [*P. glandulosa* and its allies. 26–124; *P. gracilis* and its allies, 125–175; *P. Drummondii* and *P. Breweri*, 176–195.]

DANSEREAU, P. Studies in *Potentillae* of high latitudes and altitudes. Trans. Roy. Soc. Canada III. Sect. 5. **49**: 11–23. 1955. [Includes list of arctic and alpine spp.; discussion of important characteristics of genus.]

ELKINGTON, T. T. Cytotaxonomic variation in *Potentilla fruticosa* L. New Phytol. **68**: 151–160. 1969.

——— & S. R. J. WOODELL. Biological flora of the British Isles: *Potentilla fruticosa* L. Jour. Ecol. **51**: 769–781. 1963.

FERNALD, M. L. The representatives of *Potentilla anserina* in eastern America. Rhodora **11**: 1–9. 1909. [3 spp. recognized.]

———. *Potentilla canadensis* and *P. simplex.* Rhodora **33**: 180–191. *pls. 214, 215.* 1931.

GENTSCHEFF, G., & Å. GUSTAFSSON. Parthenogenesis and pseudogamy in *Potentilla.* Bot. Not. **1940**: 109–132. 1940.

GREWAL, M. S., & J. R. ELLIS. Sex determination in *Potentilla fruticosa.* Heredity **29**: 359–362. 1972.

GUÉDÈS, M. Premières observations sur la stipule ligulaire de quelques dicotylédons. Beitr. Biol. Pflanzen **45**: 313–327. 1968. [*P. anserina, P. fruticosa, P. reptans, P. rupestris.*]

HÅKANSSON, A. Untersuchungen über die Embryologie einiger *Potentilla*-Formen. (English summary.) Lunds Univ. Årsskr. II. **42**(5): 1–70. 1946.

HARPER, R. M. A southern outpost for *Potentilla tridentata.* Rhodora **31**: 221–223. 1929. [Blood Mt., Union Co., Georgia.]

HOLM, T. Contributions to the knowledge of the germination of some North American plants. Mem. Torrey Bot. Club **2**: 57–108. *pls. 5–19.* 1891. [*P. canadensis*, 70.]

HUNZIKER, H. R. Beitrag zur Aposporie und ihrer Genetik bei *Potentilla.* (English summary.) Arch. Julius Klaus-Stiftung **29**: 135–222. *pl. 1.* 1954.

KALKMAN, C. *Potentilla, Duchesnea,* and *Fragaria* in Malesia (Rosaceae). Blumea **16**: 325–354. 1968.

KECK, D. D. Revision of *Horkelia* and *Ivesia.* Lloydia **1**: 75–142. 1938. [Includes discussion on generic delimitation of *Potentilla.*]

KELLEY, W. R. Study of seed identification and seed germination of *Potentilla* spp. and *Veronica* spp. N.Y. State Agr. Exper, Sta. Mem. **317.** 31 pp. 1953.*

LEBÈGUE, A. Polyembryonie chez le *Potentilla aurea* L. Bull. Soc. Bot. France **97:** 199–201. 1950. [See also SOUÈGES, *ibid.* **82:** 381–384. 1935, for polyembryony in *P. reptans.*]

LISTOWSKI, A. Observations on plant development (IX). The development of *Potentilla supina.* (In English; Polish summary.) Acta Soc. Bot. Polon. **34:** 1–26. *1 table.* 1965. (XIV). Interactions between seedling time, age of plant, vernalization length and florescence of *Potentilla supina. Ibid.* **36:** 449–458. 1967.

LÖVE, Á. Cytotaxonomical remarks on some American species of circumpolar taxa. Sv. Bot. Tidskr. **48:** 211–232. 1954. [*P. fruticosa*, sensu lato, segregated as *Pentaphylloides*, N. Am. form called *P. floribunda* (Pursh) Á. Löve; *P. norvegica.*]

MATFIELD, B., & J. R. ELLIS. The allopolyploid origin and genomic constitution of *Potentilla anglica.* Heredity **29:** 315–327. *pl. 1.* 1972. [A segmental allopolyploid between *P. reptans* and *P. erecta.*]

———, J. K. JONES, & J. R. ELLIS. Natural and experimental hybridization in *Potentilla.* New Phytol. **69:** 171–186. 1970.

MÜNTZING, A. The balance between sexual and apomictic reproduction in some hybrids of *Potentilla.* Hereditas **44:** 145–160. 1958. [*P. argentea* complex.]

———. Heteroploidy and polymorphism in some apomictic species of *Potentilla. Ibid.* 280–329.

———. Further studies on intraspecific polyploidy in *Potentilla argentea* (coll.) Bot. Not. **111:** 209–227. 1958.

PAWLOWSKI, B. De generis *Potentilla* L. serie *Crassinerviae* (Th. Wolf) B. Pawl. nec non de taxis affinibus. (In Latin; Polish summary.) Frag. Fl. Geobot. **11:** 53–91. *figs. 19–22.* 1965.

POPESCU, A. Consideratii taxonomice si filogenetice asupra sectiei *Rectae* (Th. Wolf) Juz. a genului *Potentilla* L. Stud. Cercet. Biol. Bucuresti Bot. **20**(1): 39–46. 1968.*

ROUSI, A. Biosystematic studies on the species aggregate *Potentilla anserina* L. Ann. Bot. Fenn. **2:** 47–112. 1965. [3 subspp. recognized.]

RUTISHAUSER, A. Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen. 245 pp. Springer-Verlag, Vienna & New York. 1967. [Includes material from, and references to, the author's earlier work on *Potentilla.*]

SHAFRANOVA, L. M. The anatomical structure of shoots in *Potentilla fruticosa* L., *P. parvifolia* Fisch. and *P. bifurca* L., associated with the transformation of shrubs into herbs in *Potentilla* L. (*s.l.*). (In Russian; English summary.) Biull. Moskov. Obshch. Ips. Pri. Biol. II. **73**(1): 140–154. 1968.

SMITH, G. L. Studies in *Potentilla* L. I. Embryological investigations into the mechanisms of agamospermy in British *P. Tabernaemontani* Aschers. New Phytol. **62:** 264–282. *pl. 6.* 1963. II. Cytological aspects of apomixis in *P. Crantzii* (Cr.) Beck ex Fritsch. *Ibid.* 283–300. *pl. 7.* III. Variation in British *P. Tabernaemontani* Aschers. and *P. Crantzii* (Cr.) Beck ex Fritsch. *Ibid.* **70:** 607–618. *pls. 1, 2.* 1971. [Part III published posthumously, prepared and augmented by V. G. BOZMAN and S. M. WALTERS.]

SOJÁK, J. Nomenklatorische Anmerkungen zur Gattung *Potentilla.* Folia Geobot. Phytotax. Bohemoslov. **4:** 205–209. 1969. [*P. supina* subsp. *paradoxa* (Nutt. ex T. & G.) Soják.]

SOUÈGES, R. Embryogénie des Rosacées. Développement de l'embryon chez le *Potentilla reptans* L. Compt. Rend. Acad. Sci. Paris **200**: 1972–1974. 1935.

TANSLEY, A. G. The nature and range of variation in the floral symmetry of *Potentilla erecta* (L.) Hampe. New Phytol. **47**: 95–110. 1948. [Flowers typically 4-merous, but 3-, 5-, and 6-merous flowers occur.]

WATSON, P. J. Evolution in closely adjacent plant populations. 6. An entomophilous species, *Potentilla erecta*, in two contrasting habitats. Heredity **24**: 407–422. 1969.

WOLF, T. Monographie der Gattung *Potentilla*. Bibliot. Bot. **16**: 1–715. *pls. 1–20. maps 1, 2.* 1908.

Tribe DRYADEAE DC.

12. **Geum** Linnaeus, Sp. Pl. 1: 500. 1753; Gen. Pl. ed. 5. 200. 1754.

Perennial herbs with rosettes terminating short, vertical rootstocks or elongated, horizontal rhizomes covered with persistent leaf bases. Basal leaves long petiolate, imparipinnately compound, mostly lyrate in outline, the terminal leaflet usually larger than the lower ones, the latter of varying sizes, some usually greatly reduced or absent, the shape and degree of division sometimes markedly different on the same plant; cauline leaves similar to basal ones, but less compound and with shorter petioles, often simple in the inflorescences; stipules of the basal leaves adnate for their entire length to the petioles and forming membranaceous wings, those of the cauline leaves free. Inflorescences terminating stems arising from the rosettes, the flowers in several- to many-flowered open cymes [rarely solitary]. Flowers white, yellow or pinkish [to orange or purple], perfect, mostly 5-merous. Calyx with an epicalyx, rarely without; calyx lobes erect, spreading, or reflexed at anthesis, commonly reflexed in fruit, green [or reddish]; floral cup saucer-shaped [to campanulate or short-cylindric], free from carpels, a small to prominent nectar ring surrounding mouth of floral cup or at base of carpels. Petals spreading [or erect] at anthesis, deciduous, shorter than to exceeding calyx lobes, narrowly to broadly elliptic, nearly circular or spathulate, the apices rounded to emarginate, the bases rounded, narrowed, or rarely distinctly clawed, inserted at outer edge of floral cup, imbricate. Androecium of 20 to many stamens in several series; filaments glabrous [or pubescent], usually persistent, perigynous on floral cup at outer edge of nectar ring [or on the sides of the floral cup]; anthers yellow. Gynoecium of several to very many free, glabrous, or pubescent, sessile [or stalked] carpels on a hemispheric to nearly globose or cylindric, glabrous or hirsute, sometimes stipitate receptacle; styles terminal, entire and wholly persistent or jointed and geniculate near or above the middle with the apical part deciduous, leaving a hooked rostrum on the fruit; stigmas terminal, punctiform; each carpel with a single, basal, upright-apotropous ovule, the micropyle inferior. Fruit an aggregation of achenes with long, straight or hooked glabrous or plumose persistent styles, the receptacle not enlarging but sometimes elevated above the calyx on an elongated stipe; seeds erect, the radicle inferior, the seed coat membranaceous. Base chromosome number 7. (Including *Acomastylis* E. L. Greene, *Stylipus* Raf., and *Sieversia* Willd.) LECTOTYPE SPECIES: *G. urbanum* L.; see Britton & Brown, Fl. No. U.S. Canada ed. 2. 2: 269. 1913. (A name used by Pliny, perhaps for *G. urbanum*.) — AVENS.

About 60 species in eleven subgenera, primarily of the Northern Hemisphere, with many species of arctic or alpine regions or moist boreal forests; a few species in the mountains of South America and in southern Africa, Tasmania, New Zealand, and the Auckland Islands. Approximately 17 species in six subgenera are found in North America, all except *Geum urbanum* indigenous, and ten of them are restricted to that area; twelve species occur in eastern North America, seven in the southeastern United States. Generic delimitation and subgeneric classification are still problematical, and numerous segregate genera and several systems of division have been proposed. Important treatments of the genus are those by Rydberg (1913), Bolle, Gajewski, and Huber in Hegi.

Four species of subg. GEUM (styles geniculate and jointed near the middle or above, the upper part deciduous, leaving a hooked rostrum on the achenes; epicalyx present) occur with us. *Geum canadense* Jacq., $2n = 42$, is a variable plant with flowers with white petals that equal or exceed the calyx lobes, densely pubescent receptacles, and sharply toothed cauline leaves that only gradually become smaller and less compound toward the stem apices. The terminal portion of the basal leaves varies from simple and merely toothed to lobed, ternate, or pinnately compound. The range of this species is from Nova Scotia to North Dakota, south to Georgia, Alabama, and eastern Texas. The plant usually occurs in moist, shaded habitats, such as woods, ravines, coves, stream banks, and thickets. Fernald & Weatherby noted six recognizable trends (four varieties and two forms) with differences in the type, distribution, and density of trichomes, number of carpels per flower, and leaf morphology. Character correlations, however, are quite weak, and subspecific categories probably are unwarranted.

The closely related *Geum laciniatum* Murray, $2n = 42$ (*G. virginianum* auct. not L.), has stouter pedicels, smaller petals that rarely exceed the calyx lobes, and mostly glabrous receptacles. This species occurs only in moist places, such as meadows, rich woodlands, and the margins of ponds, streams, and ditches, from Nova Scotia and southern Ontario to Minnesota, south to North Carolina, Alabama, Illinois, Missouri, and Kansas. Plants, mostly from the southern part of the range, with sparsely hirsute, rather than glabrous, achenes have been distinguished as var. *trichocarpum* Fern. The artificial hybrid between this and the preceding species is vigorous and quite fertile. Gajewski (1957) noted that in *G. laciniatum* the achenes do not readily become detached from the receptacle, but instead the entire fruiting head is easily broken off at the base and dispersed as a unit.

Geum aleppicum Jacq., $2n = 42$, has the widest distribution of any species of *Geum*, occurring in northern Eurasia from Kamchatka and Japan to Poland, Czechoslovakia, Hungary, and Albania, and in North

America from Newfoundland and the Gaspé Peninsula to Mackenzie and British Columbia, southward to North Carolina, Ohio, Indiana, Illinois, Iowa, Nebraska, New Mexico, California, and northern Mexico. New World plants have been called var. *strictum* Fern., but the great range of variation in this species makes the recognition of subspecific taxa futile. *Geum aleppicum* can be recognized by its deep yellow to orange petals that exceed the calyx lobes, hirsute receptacles, and pinnate basal, lower, and middle leaves.

Geum virginianum L. (*G. flavum* (Porter) Bickn.; *G. hirsutum* Muhl.), $2n = 42$, is very similar to *G. canadense*, but differs in the cream-colored to pale yellow petals that are shorter than the calyx lobes and in the larger stipules. This species occurs in dry to moist upland woods and thickets from Massachusetts to Indiana, south to South Carolina, Tennessee, and Kentucky. Raynor and Gajewski indicate that *G. virginianum* may have originated by hybridization between *G. canadense* and *G. aleppicum*. Plants of true *G. virginianum* are quite fertile and show no segregation in subsequent generations. The artificial F_1 hybrid between *G. canadense* and *G. aleppicum*, while morphologically similar to *G. virginianum*, is highly sterile. Some herbarium specimens assignable to *G. virginianum* have mostly aborted pollen and may represent natural hybrids; these are mostly from north of our area where *G. canadense* and *G. aleppicum* are sympatric.

Geum geniculatum Michaux is a poorly known species restricted to balds, shaded coves, and moist woods on the upper slopes of Roan and Grandfather mountains in western North Carolina and eastern Tennessee, where it is locally abundant. Nodding flowers, spathulate petals that are truncate or emarginate above and clawed below, and plumose styles that exceed the calyx lobes at or soon after anthesis (the terminal stylar portion as long as or longer than the beak portion) characterize this species, which is quite similar to the circumpolar *G. rivale* L., $2n = 42$, but which differs from it by the spreading (not strongly ascending) perianth, greenish (not purple) floral cups, and hemispheric and sessile (instead of globose and stipitate) fruiting aggregates. Gajewski (1957) thinks that *G. geniculatum* is a hybrid, with *G. rivale* being one parent. It cannot, however, be a first generation hybrid, since the nearest station for *G. rivale* is in West Virginia. The percentage of pollen stainability of *G. geniculatum* is very high.

The only species of subg. STYLIPUS (Raf.) Torrey & Gray is *Geum vernum* (Raf.) Torrey & Gray (*Stylipus vernus* Raf.), $2n = 42$, which occurs in moist, rich woods, swamp forests, and shaded valleys from New York and southern Ontario to Michigan and Iowa, southward to North Carolina, Tennessee, Kentucky, Arkansas, and eastern Texas. This species has very small flowers with cream-colored to yellow petals, a floral cup that lacks an epicalyx, sepals that are strongly reflexed at anthesis, and an aggregation of achenes that is elevated on a stipe above the calyx.

Subgenus MICRACOMASTYLIS (F. Bolle) K. R. Robertson[6] (styles straight, not jointed, basally pubescent, wholly persistent in fruit) is represented with us by *Geum radiatum* Michaux (*Sieversia radiata* (Michaux) Greene; *Acomastylis radiata* (Michaux) F. Bolle; *Parageum radiatum* (Michaux) Hara), $2n = 42$, that is endemic to balds on the high mountains of western North Carolina and eastern Tennessee. This species is easily recognized by the basal leaves with a large, reniform terminal lobe. The cauline leaves are few and much reduced in size. Its relatives are *G. Peckii* Pursh (White Mountains, of New Hampshire, and Brier Island, western Nova Scotia), $2n = 42$; *G. Schofieldii* Calder & Taylor (Queen Charlotte Islands, British Columbia), $2n = 112$; *G. calthifolium* Smith (Japan and Kamchatka to Alaska and British Columbia), $2n = 42$; and two species of China and the Himalayas.

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[6] *Geum* subgenus **Micracomastylis** (F. Bolle) K. R. Robertson, comb. nov. *Acomastylis* E. L. Greene subg. *Micracomastylis* F. Bolle, Repert. Sp. Nov. Beih. 72: 85. 1933; including *Acomastylis* subg. *Megacomastylis* F. Bolle. LECTOTYPE SPECIES:

Geum, *Waldsteinia*, and *Coluria* R. Br. (5 spp. of China and southern Siberia) are closely related and form a distinctive unit ("Geinae" of Schulze-Menz in Melchior; tribe Geeae sensu Gajewski) of tribe Dryadeae DC. (mostly shrubs and perennial herbs; styles terminal, elongated; each carpel with one (exceptionally two) basal, erect-apotropous ovule; fruit an aggregation of achenes). Other members of this tribe are *Dryas* (Holarctic; 3 or more species [numerous local forms have been given specific status]), *Cowania* D. Don (about six species of the southwestern United States and Mexico), *Fallugia paradoxa* (D. Don) Endl. (southwestern North America), *Chamaebatia* Bentham (2 spp. of California and Baja California), *Purshia* DC. (two spp.; Oregon to Wyoming and Colorado, California, and Mexico), and *Cercocarpus* HBK. (10 or more species; Oregon to western Kansas southward to Mexico). The ovule type of these genera was used by Juel to segregate them as a distinct subfamily, Dryadoideae (DC.) Juel.

Within tribe Dryadeae are found adaptations that evidently resulted from a change from insect to wind pollination. Most species of *Geum* and *Waldsteinia* have complete perianth whorls and punctiform stigmas and are insect pollinated. The flowers of *Cercocarpus* species are apetalous, with the stigmatic area forming a crest on the styles, and are presumably anemophilous. Some other genera of the tribe are intermediate between these extremes. Several dispersal mechanisms also occur in the tribe. Species of *Geum* subg. GEUM and STYLIPUS have an achene surmounted by a hooked rostrum that catches in the fur of mammals (and the clothing of botanists). In *G. heterocarpum* Boiss., $2n = 28$ (Spain and northern Africa and disjunct in Asia Minor and Central Asia) the rostrum is straight and bears many retrorse, apical bristles. Other species of *Geum*, and members of *Dryas*, *Cowania*, *Fallugia*, and *Cercocarpus*, are wind dispersed by their elongated, persistent, plumose styles. The achenes of *Waldsteinia*, *Chamaebatia*, *Coluria*, and *Purshia* have no obvious dispersal mechanisms and are perhaps eaten by birds and small mammals or carried by ants. Some (or all?) species of *Cercocarpus*, *Dryas*, and *Purshia* have nitrogen-fixing root nodules (see Rodriguez-Barrueco, family ref.).

G. Rossii (R. Br.) Ser. in DC.; see P. A. Rydberg, N. Am. Fl. **22**: 401. 1913. Gajewski's use of *Acomastylis* Greene at the subgeneric level under *Geum* is superfluous.

The base chromosome number in *Geum*, *Waldsteinia*, and *Coluria* is 7. In the other genera of Dryadeae it is 9, and only diploids are known. Most species of *Geum* thus far known cytologically are hexaploid with $2n = 42$. Relatively few species are tetraploid, octoploid, decaploid, or 12-ploid, and no diploids have been reported. The highest chromosome number reported for the genus is $2n = 112$ for *G. Schofieldii*. The chromosomes of *Geum* species are mostly small and uniform in size and shape.

The species of *Geum* are mostly quite distinct and show considerable differentiation in gross morphology, degree of polyploidy, and geographic distribution; yet barriers to artificial hybridization are nearly nonexistent in subg. GEUM, and many intersubgeneric crosses can be made. Gajewski's extensive studies indicate that the ability of two species to hybridize generally does not appear to be correlated with systematic relationship, chromosome number, direction of the cross, or biotypes used. There is, however, considerable variation in the viability and fertility of the interspecific hybrids.

The inheritance of certain morphological traits has also been studied by Gajewski. The presence of anthocyanin pigments in *Geum rivale* is due to a single dominant gene. Perhaps three allelomorphic genes determine petal color: one gene either allows the expression of the other genes or suppresses them (the petals are then white), another gene determines cream-colored petals, and the remaining gene red petals. Yellow petals occur when the genes for "color," "red," and "cream" are homozygous in the same plant. Petal apices are controlled by one gene, with "emarginate" dominant over "rounded." In F_1 hybrids between *G. montanum* L. $2n = 28$ (styles straight, pinnately plumose, entirely persistent), and species of subg. GEUM, a variety of stylar types occurs in the same individual or flower. In the second generation, most plants have hooked styles, but "montanum" and intermediate type styles occur infrequently. (Gajewski postulates that subg. GEUM is of amphiploid origin between species related to *G. montanum* and *Waldsteinia*.)

REFERENCES:

Under subfamily references see JACKSON and SCHAEPPI & STEINDL; under family references see BOUTINEAU, BUNTING, CHUTE, DEVADAS & BECK, HARA, HEGI, HUBER (1961–1966), HULTÉN (1958, 1971), LÖVE & LÖVE, LUBBOCK, RICKETT, ROBERTSON, and ROSS-CRAIG.

BOLLE, F. Eine Übersicht über die Gattung *Geum* L. und die ihr nahestehenden Gattungen. Repert. Sp. Nov. Beih. **72:** 1–119. 1933.

BUCHERER, E. Ueber Prolification und Phyllodie bei *Geum rivale*. Ber. Deutsch. Bot. Ges. **10:** 571–576. *pl. 29.* 1892.

CHEYMOL, J. Variations dans la composition glucidique de la racine de Benoîte (*Geum urbanum* L.) au cours de la végétation d'une année. Bull. Soc. Chim. Biol. **13:** 470–476. 1931.

FERNALD, M. L. Critical plants of the upper Great Lakes region of Ontario and Michigan (continued). Rhodora **37:** 273–301. *pls. 363–375.* 1935. [*Geum,* 292–295, *pls. 368–370.*]

——— & C. A. Weatherby. Varieties of *Geum canadense*. *Ibid.* **24**: 47–50. 1922. [6 recognizable, morphological trends; 4 vars., 2 forms.]

Gajewski, W. A cytogenetic study on the genus *Geum* L. Monogr. Bot. **4**: 3–416. *pls. 1–4.* 1957. [Major taxonomic and cytogenetic paper on *Geum*; many subgeneric names invalidly published.]

———. Evolution in the genus *Geum*. Evolution **13**: 378–388. 1959. [Morphological, geographical, cytological, hybridization, and genetical data used to trace evolutionary history of genus.]

———. The heredity of seed-dispersing mechanisms in *Geum*. Genetics today, Proc. 11th Int. Congr. Genet. 1963. **2**: 423–430. 1965. [*G. rivale*, *G. montanum*, and their hybrids.]

Grigorescu, E. Pharmakognostiche Studie über das Rhizom von *Geum urbanum* und Bestimmung der Gerbstoffe. Farmacia **4**: 226 +. 1956.* [Also see **6**: 441. 1960.*]

Hooker, W. J. *Sieversia Peckii.* Mr. Peck's Sieversia. Bot. Mag. **55**: *pl. 2863.* 1828. [= *G. Peckii.*]

Iltis, H. Über das Gynophor und die Fruchtausbildung bei der Gattung *Geum*. Sitz-ber. Akad. Wiss. Math.-Naturw. Wien. Abt. I. **122**: 1177–1212. *pls. 1, 2.* 1913.

Juguet, M. Polyembryonie chez le *Geum rivale* L. Bull. Soc. Bot. France **113**: 133–137. 1966.

——— & A. Lebègue. Développement de l'embryon chez les *Geum rivale* et *Geum reptans*. Compt. Rend. Acad. Sci. Paris **261**: 4814–4817. 1965.*

Kowal, T., & A. Krupińska. The diagnostic characters of fruits and seeds of *Geum* L. species. (In Polish; extensive English summary.) Monogr. Bot. **29**: 69–120. 1969. [26 spp.; key to species using fruit and seed characters; illustrations.]

Král, M. Die Begrenzung der Gattung *Parageum* Nakai et Hara. Preslia **38**: 151–153. 1966. [2 subgenera, 2 sects., and 2 series recognized.]

Marsden-Jones, E. M. The genetics of *Geum intermedium* Willd. haud Ehrh., and its back-crosses. Jour. Genet. **23**: 377–395. *pls. 12–15.* 1930.

McArthur, I. C. S., & T. A. Steeves. An experimental study of vascular differentiation in *Geum chiloënse* Balbis. Bot. Gaz. **133**: 276–287. 1972. [= *Geum* 'Mrs. Bradshaw.']

Phelouzat, R. Morphologie, phyllotaxie, ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26**: 101–362. 1963.*

Pšenák, M., A. Jindra, P. Kovács, & H. Dulovcová. Biochemical study on *Geum urbanum*. Pl. Med. **19**: 154–159. 1970.

Raynor, L. A. Cytotaxonomic studies of *Geum*. Am. Jour. Bot. **39**: 713–719. 1952. [Based on a doctoral dissertation submitted to Cornell Univ. in 1945.]

Schneider, G. H., Jr. *Geum canadense*, a study of its seasonal periodicity in New Jersey. Castanea **17**: 117–128. 1952.

Schulthess, H. Pharmakognostisch-anatomische und chemische Untersuchungen von Drogen des Genera *Geum*, *Sieversia* und *Dryas*. Thesis, Zurich. 114 pp. 1945.*

Souèges, R. Embryogénie des Rosacées. Les premiers stades du développement de l'embryon chez le *Geum urbanum* L. Compt. Rend. Acad. Sci. Paris **174**: 1070–1072. 1922; Les derniers stades du développement de l'embryon chez le *Geum urbanum* L. *Ibid.* 1197–1199.

———. Développement de l'embryon chez le *Geum urbanum* L. Bull. Soc. Bot. France **70:** 645–660. 1923.

13. **Waldsteinia** Willdenow, Neue Schr. Ges. Naturf. Freunde Berlin 2: 105. *pl 4, fig. 1.* 1799.

Low, perennial, colonial herbs with the aspect of strawberry plants, the leaves in basal rosettes from crowns on slender subterranean rhizomes at the time of flowering, but (at least in *W. fragarioides*) the rosettes later elongating and the leaves cauline by autumn; roots adventitious along monopodially branching rhizomes; indumentum of long and short, simple as well as multicellular-glandular trichomes. Leaves ternately compound or palmately 3–5-lobed, long petiolate, the leaf blades or leaflets variously toothed and incised; stipules adnate to petiole for nearly their entire length, forming membranaceous, reddish wings at base of petiole; lower part of petioles and stipules persistent on the rhizomes. Inflorescences loose, long pedunculate, few-flowered cymes arising from the rosettes; bracts small, deltoid, entire to slightly 3-lobed [or foliaceous]. Flowers light to bright yellow, the centers often more intensely colored, perfect. Calyx with or without an epicalyx; calyx lobes 5, triangular-lanceolate, persistent, valvate in aestivation; floral tube obconic, free of the carpels, a lobed nectar ring nearly covering the mouth of the floral tube. Petals 5, spreading, deciduous, narrowly to broadly ovate, very short clawed with 2 basal auricles in *W. geoides*, inserted at the edge of the floral tube, quincuncial cochlear. Androecium of 25–80 stamens; filaments slender, in several series, persistent, perigynous around the periphery of the floral tube; anthers yellow. Gynoecium of 2–6 (rarely more) free, pubescent, distinctly stalked, superior carpels; styles terminal, articulated at the bases and wholly caducous; stigmas terminal, punctiform; each carpel with a single, basal, erect-apotropous ovule. Accessory fruits dry, surrounded by the persistent calyx and filaments, the receptacle not enlarging. Achenes dry, pubescent, plump, obovoid; embryo erect, the radicle inferior. Base chromosome number 7. TYPE SPECIES: *W. geoides* Willd. (Named in honor of Graf Franz de Paula Adam von Waldstein-Wartenberg, 1759–1823.) — BARREN STRAWBERRY.

Five species distributed in an Arcto-Tertiary relict pattern with *Waldsteinia geoides*, $2n = 14$, the only species of subg. WALDSTEINIA, in Bulgaria, Yugoslavia, Rumania, southwestern Ukraine, Czechoslovakia, and Hungary; *W. fragarioides* (Michx.) Tratt. in the eastern, and *W. lobata* (Baldwin in Elliott) Torrey & Gray in the southeastern United States; *W. idahoënsis* Piper in west-central Idaho; and *W. ternata* (Stephen) Firsch in three widely separated areas: subsp. *ternata* along the southeastern shore of Lake Baikal in eastern Siberia; subsp. *Maximowicziana* Teppner, $2n = 42$, in Sakhalin, the Amur and Ussuri river regions, Manchuria, North Korea, and Japan; and subsp. *trifolia* (Rochel ex Koch) Teppner, $2n = 28, 35, 42$, in Austria, Rumania, and Czechoslovakia. The last four species comprise subg. COMAROPSIS (Richard in Nestler) Teppner. The taxonomy used here is that adopted by Teppner in his recent revision of the genus.

Waldsteinia fragarioides (leaves ternately compound, epicalyx lobes either absent or small and occurring only between some calyx lobes, pedicels with red-capped glandular trichomes of two lengths) ranges from New Brunswick and Maine to Ontario and Minnesota, southward to Georgia, Alabama, and Missouri. A northern and a southern subspecies can be distinguished. Subspecies *fragarioides*, with the petals broadly obovate or elliptic and greatly exceeding the calyx lobes, occurs in woods, thickets, and clearings from the northern limit of the species to southwestern Virginia, Ohio, Indiana, and southern Missouri; this taxon probably enters our area in the mountains of northwestern North Carolina. Two chromosomal races are known, diploid ($2n = 14$), reported from Ontario and Pennsylvania, and triploid ($2n = 21$), known from localities in Quebec, Ontario, New York, and Pennsylvania. The southern subsp. *Doniana* (Tratt.) Teppner (*W. Doniana* Tratt., *W. parviflora* Small, *W. fragarioides* var. *parviflora* (Small) Fernald) has petals that are narrower and shorter than the calyx lobes. It is restricted to the mountains and Piedmont of North and South Carolina, southern Kentucky, Tennessee, and northern Alabama and Georgia. *Waldsteinia fragarioides* and *W. ternata* are quite similar morphologically and form a pair of closely related vicarious species, as noted by Gajewski.

Waldsteinia lobata is a very poorly known species endemic to the Piedmont of Georgia and adjacent South Carolina. Both *W. lobata* and its close relative *W. idahoënsis*, an endemic of the Bitter Root Mountains in Idaho, have three- to five-lobed leaves and calyces that lack epicalyx lobes; in *W. lobata* the petals are about the same length as and narrower than the calyx lobes, while in *W. idahoënsis* the petals much exceed the calyx lobes in both length and width. Chromosome counts are lacking for these two species, but Teppner (1968) notes that the larger pollen grains frequently with four instead of three colpi in *W. idahoënsis* suggest a higher ploidy level in that species than in *W. lobata*. Gajewski thought that *W. lobata* and *W. geoides* were allied vicarious species. However, although both species have lobed rather than compound leaves, they differ in numerous floral details, and Teppner placed them in distinct subgenera.

The only confirmed interspecific hybrid is *Waldsteinia* × *Vranyi* Hendrych (*W. geoides* × *W. ternata* subsp. *trifolia*).

The genus is of little economic importance. Some species, particularly *Waldsteinia ternata* and *W. fragarioides*, are cultivated as ground covers, used in edging borders, or grown in rock gardens.

REFERENCES:

Under subfamily references see JACKSON and NESTLER; under family references see BUNTING, CHITTENDEN, CHUTE, HUBER (1961–1966), RICKETT, and WOOD.

FERNALD, M. L. Critical plants of the upper Great Lakes region of Ontario and

Michigan (cont.). Rhodora **37**: 272–301. *pls. 363–375.* 1935. [*Waldsteinia,* 285, 286.]

GAJEWSKI, W. A cytogenetic study on the genus *Geum* L. Monogr. Bot. **4**: 1–416. 1957. [Includes review of related genera; for *Waldsteinia* see particularly pp. 7–15, 99–105, 115, 116.]

———. Evolution in the genus *Geum.* Evolution **13**: 378–388. 1959. [Includes *Waldsteinia.*]

HOOKER, W. J. *Dalibarda lobata.* Hooker's Ic. Pl. **1**: *pl. 76.* 1837. [= *W. lobata.*]

MULLIGAN, G. A., & B. R. BAUM. *In*: Á. Löve, IOPB chromosome number reports XXVIII. Taxon **19**: 608–610. 1970. [*W. fragarioides,* $2n = 14$ (Ontario and Pennsylvania) and $2n = 21$ (Quebec, Ontario, and Pennsylvania).]

SIMS, J. *Dalibarda fragarioides.* Strawberry-leaved Dalibarda. Bot. Mag. **38**: *pl. 1567.* 1813. [= *W. fragarioides* subsp. *Doniana.*]

TEPPNER, H. Zur Kenntnis der Gattung *Waldsteinia.* 1. Schlüsel zum Bestimmen von Rosaceen-Pollen einschliesslich ähnlicher Pollenformen aus anderen Familien. Phyton Austria **11**: 224–238. 1966.

———. Zur Kenntnis der Gattung *Waldsteinia.* Inaug. Diss., Karl-Franzens-Univ., Graz. 129 pp. + *39 pl.* Graz. 1968. [World-wide revision.]

WALDSTEIN, F. P. A. VON, & P. KITAIBEL. *Waldsteinia geoides.* Descr. Ic. Pl. Hungariae **1**: 79. *pl.* 77. 1801 or 1802.

Tribe SANGUISORBEAE Juss. [rank assigned by DC. Prodr. **2**: 588. 1825].

14. **Agrimonia** Linnaeus, Sp. Pl. 1: 448. 1753; Gen. Pl. ed. 5. 206. 1754.

Perennial herbs with erect stems arising from stout horizontal rhizomes, stems mostly unbranched below the inflorescences; roots coarse, fibrous, sometimes with fusiform thickenings; indumentum of simple and/or glandular trichomes, the density various. Leaves imparipinnate, the basal leaves rather small, not persistent, the cauline ones with small leaflets interspersed between large leaflets, the leaflets sharply toothed or lobed; stipules of the basal leaves elongate, adnate to either side of the petiole and forming a dilated wing, the apices free, acuminate, the margins with few or no teeth, those of the cauline leaves larger and broader, only basally adnate to the petiole, the margins deeply toothed or divided. Inflorescences several elongate racemes terminating the main stems, the flowers nearly sessile, the pedicels ascending in flower, spreading or descending in fruit, subtended by a small bract, the floral cup with 2 small bractlets beneath. Flowers small, 5-merous. Calyx without an epicalyx, the lobes spreading at anthesis, becoming incurved and forming a beak on the fruit; floral cup turbinate to hemispheric, the throat constricted, the outer rim of the cup with numerous hooked bristles that elongate and stiffen in fruit; nectar ring prominent, conical, nearly closing the mouth of the floral cup. Petals yellow, small, oval to orbicular, without claws, caducous. Androecium of 5–15 stamens; filaments slender, inserted at the outer edge of the nectar ring; anther locules somewhat separated by the broad connectives. Gynoecium of 2 separate carpels inserted at the base of, and free from, the floral cup; styles terminal; stigmas terminal, somewhat 2-lobed; each carpel with a solitary, anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit accessory, of 2 achenes inclosed within the enlarged, hardened, usually 10-grooved floral cup, the bristles stiff, hooked, reflexed to ascending; each achene with a single seed, the seed coat membranaceous, the radicle superior. Base chromosome number 7. TYPE SPECIES: *A. Eupatoria* L.; see Linnaeus, Gen. Pl. ed. 5. 206. 1754.[7] — AGRIMONY.

About 18 species with ten in North America (seven in our area), two in eastern South America, two confined to eastern Asia, *A. repens* L., $2n = 28$, in Anatolia (naturalized in other parts of Europe), *A. procera* Wallroth (*A. odorata* auct.), $2n = 56$, in Europe, *A. Eupatoria* L., $2n = 28$, with three subspecies extending from Europe to central and southwestern Asia, and *A. pilosa* Ledeb., $2n = 56$, that ranges from eastern Europe to the Himalayas, China, Siberia, and Japan. The genus is being revised by Vladimír Skalický, who groups the species into five series and several subseries.

Agrimonia gryposepala Wallroth, $2n = 56$, the only member of series *Procerae* Skalický in our area, ranges from Prince Edward Island to Ontario, northern Michigan and North Dakota, southward to New Jersey, Pennsylvania, Indiana, Missouri, eastern Kansas, and Louisiana, and in the mountains of eastern Tennessee and western North and South Carolina. This species, readily distinguished from others in the Southeast by its larger fruits (to 8 mm. long) and the minutely glandular inflorescence branches, prefers moist habitats, such as thickets, woodlands, and the borders of woods; with us it is found mostly in bogs, meadows, and low pastures. *Agrimonia macrocarpa* Rydb., of Mexico, and *A. procera*, of western, central, and southern Europe, are allied species.

Series *Tuberosae* Skalický, named for the fusiform-thickened roots, is strictly American, and all four species are found with us. *Agrimonia pubescens* Wallroth (*A. mollis* (Torrey & Gray) Britton), with cauline indumentum of long, incurving, eglandular trichomes, lower leaves with mostly 5 to 7 (rarely 9), elliptical leaflets, and mature fruits 2.5–5 mm. long, ranges from New England, southern Ontario, Michigan, and Minnesota to the Carolinas, Tennessee, Georgia, Alabama, Mississippi, Missouri, Arkansas, eastern Kansas, and Oklahoma, occurring in rather dry, often calcareous habitats. The very similar *A. Bicknellii* (Kearney) Rydb. (Massachusetts, New York, Michigan, and Illinois, to New Jersey, Pennsylvania, North Carolina, Tennessee, and Georgia) is often merged with *A. pubescens*. It differs from *A. pubescens* in the greater number of leaflets (usually 7 to

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[7] In the *Species Plantarum*, Linnaeus distinguished two species, *A. Eupatoria* and *A. Agrimonoides*, and in the *Genera Plantarum* two subgeneric categories, *Agrimoniae* and *Agrimonoidis*. According to Article 22 of the International Code of Botanical Nomenclature, "when the epithet of a subdivision of a genus is identical with or derived from the epithet of one of its constituent species, this species is the type of the name of the subdivision of the genus . . . ." The subgeneric category *Agrimonoidis* is based on *A. Agrimonoides*, which is thus its type. Therefore, *A. Eupatoria* is the type of the subgeneric taxon *Agrimoniae* and the genus *Agrimonia*. De Candolle (Prodr. 2: 588. 1825) later removed *A. Agrimonoides* to the genus *Aremonia* Necker ex Nestler.

13) and in the spreading instead of ascending bristles on the fruit. *Agrimonia microcarpa* Wallroth (*A. pubescens* var. *microcarpa* (Wallroth) Ahles; including *A. platycarpa* Wallroth and *A. pumila* (Muhl.) Bicknell) is a woodland species with a more southern distribution (Pennsylvania, New Jersey, southward to the Virginias and Carolinas, Kentucky, Tennessee, Georgia, and Florida, and westward to eastern Texas). It is distinguished by the longer, more spreading trichomes on the stems, the fewer leaflets per leaf (3 to 5 or rarely 7), and the smaller fruits (1.5 to 3 mm. long). These three species are grouped by Skalický in his subseries *Tuberosae.* The only species of subseries *Rostellatae* Skalický is *A. rostellata* Wallroth (*A. striata* sensu Bicknell), which occurs in open woods from southern New England, New York, Ohio, Indiana, Illinois, Missouri, and eastern Kansas, southward to the Carolinas, Georgia, Oklahoma and eastern Texas. It is characterized by an indumentum of glandular trichomes and small fruits with the calyx lobes exceeding the short ascending or spreading bristles.

Series *Parviflorae* Skalický has an unusual geographical distribution: two species in eastern North America and two poorly known species, *A. villosa* Cham. & Schlecht. and *A. hirsuta* Bongard in Meyer in southeastern Brazil. *Agrimonia parviflora* Aiton, a plant of moist, open areas, is found from Florida to Texas north to Connecticut, New York, southern Ontario, Michigan, Illinois, Iowa, and Nebraska. It occurs disjunctly on Hispaniola. This is a rather coarse plant with spreading, long-villous stems, and leaves that have 11 to 15 abaxially glandular-dotted, lanceolate large leaflets and numerous small leaflets per leaf. *Agrimonia incisa* Torrey & Gray, quite similar but with deeply incised leaflets only 1 to 3 cm. long, is restricted to pine woods from South Carolina to Florida, and Mississippi. This series is supposed to lack fusiform-thickened roots, but at least one collection (*Curtiss 753* [GH], dry pine woods near the Santee Canal, South Carolina), definitely has such roots.

Fourteen genera comprise tribe Sanguisorbeae (carpels one to four, rarely to ten, inclosed by, but not adnate to, the urceolate floral cup; fruits achenes inclosed by the usually dry and hardened floral cups that frequently have spines or marginal wings; ovules solitary; stamens 15 or fewer, rarely to ca. 50; leaves mostly imparipinnate); the tribe is particularly diverse south of the Tropic of Cancer in South America and Africa. The genera can be placed in three groups (variously treated as tribes or subtribes: *Agrimonia* and related genera; *Alchemilla*; and *Sanguisorba* and congeners. Genera allied to *Agrimonia* are *Aremonia* Necker ex Nestler, nom. cons. (*A. agrimonoides* (L.) DC., central and southern Europe); *Spenceria* Trimen (two species, China); *Hagenia* J. F. Gmelin (*H. abyssinica* (Bruce) J. F. Gmelin, tropical Africa); and *Leucosidea* Ecklon & Zeyher (*L. sericea* Ecklon & Zeyher, South Africa).

REFERENCES:

Under subfamily references see SCHAEPPI & STEINDL; under family references see Bate-Smith, Boutineau, Bunting, Chute, Hegi, Lubbock, Rickett, Robertson, and Ross-Craig.

Alexander, E. J. *Agrimonia gryposepala.* Addisonia **17:** 19, 20. *pl. 554.* 1932.

Bicknell, E. P. The North American species of *Agrimonia.* Bull. Torrey Bot. Club **23:** 508–523. *pls. 282, 283.* 1896. [Comments by B. L. Robinson on the nomenclature used by Bicknell are found in Rhodora **2:** 235–238. 1900, and Bull. Torrey Bot. Club **28:** 295–300. 1901; retorts by Bicknell in Bull. Torrey Bot. Club **28:** 102–108, 514–518. 1901.]

Brittan, N. H. Cytotaxonomy of some species of *Agrimonia* L. (Abstract.) Proc. VII Int. Bot. Congr. **1950:** 278. 1953.*

Gams, H. *Agrimonia. In:* G. Hegi, Ill. Fl. Mittel-Europa, ed. 1. **4**(2): 930–935. 1922.

Hara, H., & S. Kurosawa. Cytotaxonomical notes on some Asiatic species of *Agrimonia.* Jour. Jap. Bot. **43:** 392–400. *pls. 20, 21.* 1968.

Madan, C. L., & B. C. Kundu. Pharmacognosy of the root of *Agrimonia Eupatoria* Linn. Jour. Sci. Industr. Res. C. **20**(12): 348–350. 1961.*

Phelouzat, R. Le méristème apical d'*Agrimonia Eupatoria* L. dans l'ontogénie de la pousse végétative et de l'inflorescence. Compt. Rend. Acad. Sci. Paris **245:** 2525–2528. 1957.

———. Morphologie, phyllotaxie et ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26:** 101–362. 1963.*

Skalický, V. Ein Beitrag zur Erkenntnis der europäischen Arten der Gattung *Agrimonia* L. Acta Horti Bot. Pragensis **1962:** 87–108. 1962.

———. Amerikanische Odermennige *Agrimonia* L. ser. *Parviflorae* ser.n. Novit. Bot. Univ. Carolinae Pragensis **1970:** 9–16. 1971. [*A. incisa* and *A. parviflora.*]

———. Diagnoses, conspectus et claves analyticae taxorum infragenericorum novorum generis *Agrimonia* L. adhusca rite non publicatorum. *Ibid.* **1971:** 13–22. 1972.

———. Miscellanea taxonomica et nomenclatorica ad generis *Agrimonia* L. investigationem pertinentia. *Ibid.* **1972:** 11–18. 1973.

———. Amerikanische Arten der Gattung *Agrimonia* L. ser. *Tuberosae* ser. nova. Folia Geobot. Phytotax. **8:** 95–104. 1973. [Includes *A. Bicknellii, A. microcarpa, A. pubescens, A. rostellata.*]

Svenson, H. K. Report of the Local Flora Committee. II. *Agrimonia;* III. *Quercus;* IV. *Ranunculus;* V. *Viola.* Torreya **41:** 3–7. 1941. [With plate illustrating the differences between 6 spp. of *Agrimonia.*]

Wallroth, F. W. Monographischer Versuch über die Gewächs-Gattung *Agrimonia* Celsi. Beiträge zur Botanik. Leipzig **1:** 1–61. *pl. 1.* 1842.

15. **Alchemilla** Linnaeus, Sp. Pl. 1: 123. 1753; Gen. Pl. ed. 5. 59. 1754.

Small, much branched annual [or, more commonly, moderate sized, rhizomatous, or cespitose perennial] herbs. Leaves simple [rarely compound], orbicular in outline, palmately [very rarely pinnately] lobed or dissected, short [to long] petiolate, all cauline [or also basal in rosettes]; stipules deeply divided, adnate to the bases of the petioles, those of each leaf connate, clasping the stems and inflorescences, with the appearance of a multifid perfoliate leaf [or the basal leaves with adnate but not connate stipules]. Inflorescences few flowered, sessile cymules in the axils of the leaves [or flowers rarely solitary or cymules arranged in elongate, compound panicles or corymbs]. Flowers very small, perfect, apetalous, usually 4-merous. Calyx with or rarely without an epicalyx, the epicalyx lobes minute [to larger than the calyx lobes], the calyx lobes green [yellowish] slightly spreading at anthesis, persistent, valvate in aestivation; floral tube urceolate [turbinate or campanulate], free of the carpels, the throat nearly closed by a fleshy nectar ring. Petals absent. Stamen 1 [or stamens 2–5], opposite [or alternate with] a calyx lobe; anther extrorse [or introrse]; filament short, inserted at the inner [or outer] edge of the nectar ring. Gynoecium of 1 carpel [or as many as 10], carpel(s) sessile [or short stipitate] at the base of the floral tube and included within it; style inserted at the base of the ovary, protruding above the throat of the floral tube; stigma discoid; each carpel with a single, ascending, orthotropous ovule. Fruit an achene enclosed within the dry, thin floral tube that does not greatly elongate; seed coat thin; embryo filling the seed, the radicle superior, straight, the cotyledons flattened, broadly ovoid. Base chromosome number 8. (Including *Aphanes* L., *Lachemilla* (Focke) Rydb., and *Zygalchemilla* Rydb.) LECTOTYPE SPECIES: *A. vulgaris* L.; see P. A. Rydberg, N. Am. Fl. 22: 377. 1908. (Name adopted, with a change in spelling, from Tournefort, the word evidently of Arabic origin; there have been various attempts to link the name with the possible use of plants of this genus in alchemy.)

Estimates of the number of species vary from 100 to over 1000, depending on how apomictic complexes are treated. Three subgenera can be recognized. Subgenus ALCHEMILLA (perennials; stamens 4, inserted on the outer edge of the nectar ring, alternate with the calyx lobes; anthers introrse) is primarily of the northern and alpine regions of Eurasia, but it also occurs in East Africa, Madagascar, India, Ceylon, and southeastern Asia. A few species are amphi-Atlantic, reaching Greenland, Labrador, Newfoundland, and the Maritime Provinces of Canada. Perhaps three other species are introduced into eastern North America, but none occurs in our area. Subgenus APHANES (L.) Reichenb. (annuals of low elevations, often weedy; stamen solitary, rarely paired, opposite a calyx lobe and on the inner margin of the nectar ring; anther extrorse) has been said to include 20 species and to have a disjunct distribution with species described from Europe, the Mediterranean region, eastern North America, western North America, southwestern South America, the eastern coast of South America, and Australia. However, most or perhaps even all of the "species" found outside Europe may be introductions of the European *A. arvensis* (L.) Scop. and/or *A. microcarpa* Boiss. & Reuter. The latter is found with us. This subgenus probably was confined to Europe before western man began his explorations of the world. Subgenus LACHEMILLA (Focke) Langerh. (perennials; stamens 2, rarely 3 or 4, opposite calyx lobes and inserted at the inner edge of the nectar ring; anthers extrorse), confined to high elevations in the western cordilleras of the Americas, includes about 50 species occurring from Mexico to Chile, Bolivia, and Argentina; *A. domingensis*

Urban is restricted to the Dominican Republic. These three subgenera are often given generic status, particularly in European floras, and, when only members of subg. Alchemilla and Aphanes are considered, such a treatment has merit. This position is less tenable when subg. Lachemilla is examined, since its diverse members largely bridge the discontinuities between the first two subgenera. Dr. Lily Perry monographed *Lachemilla* in 1929, treating it as a section of *Alchemilla*; she now thinks that it is generically distinct.

Alchemilla microcarpa (*Aphanes microcarpa* (Boiss. & Reuter) Rothmaler; *Aphanes australis* Rydb.), $2n = 16$, parsley-piert, a tiny winter annual of western Europe and the Mediterranean region, is naturalized in the United States from Delaware and the District of Columbia along the Piedmont and inner Coastal Plain to North Carolina, Tennessee, Georgia, Florida, Alabama, Mississippi, and eastern Texas. This species, usually occurring in open, disturbed areas and sometimes becoming a troublesome lawn weed, supposedly reproduces sexually, although it is closely allied to the facultatively apomictic *A. arvensis*, $2n = 48$.

All of the European species of subg. Alchemilla (except *A. pentaphyllea* L. and a few others) are obligate apomicts, but many of them are no more difficult to delimit than sexually reproducing species in other genera. Some are very widely distributed and, although often quite variable, retain morphological distinctions; a large number have very local or disjunct distributions, but likewise present no taxonomic difficulties. These species are high-level polyploids (to $2n =$ ca. 220, ca. 224 in *A. faroënsis* (Lange) Burser), and it has been suggested that they are complex hybrids involving now extinct sexually reproducing species.

Because of its apetalous flowers, urceolate floral tubes inclosing the solitary or few carpels, and fruits with achenes inclosed by the floral cup, *Alchemilla* is often included in tribe Sanguisorbeae Juss., along with *Agrimonia* L., *Sanguisorba* L., and about ten other genera. *Alchemilla* differs from these, however, in its palmate leaves, basal styles, basal, orthotropous ovules, and base chromosome number of 8. It is sometimes placed in its own tribe; Schulze-Menz in Melchior considered it a subtribe of his Potentilleae.

REFERENCES:

Under subfamily references see Schaeppi & Steindl; under family references see Bate-Smith, Boutineau, Bunting, Gustafsson, Hegi, Hultén (1958), Jessen, Lubbock, Rickett, and Ross-Craig.

Böös, G. Über parthenogenesis in der Gruppe *Aphanes* der Gattung *Alchemilla* nebst einigen im Zusammenhang damit stehenden Fragen. Lunds Univ. Årsskr. II. Sect. 2. **13**(4): 1–37. 1917.

———. Neue embryologische Studien über *Alchemilla arvensis* (L.) Scop. Bot. Not. **124**: 209–250. 1924.

Fernald, M. L. Noteworthy plants of southeastern Virginia (continued). Rhodora **40**: 434–459. *pls. 521–530.* 1938. [*Alchemilla,* 435, 436; eastern North American plants are *A. microcarpa*, not *A. arvensis.*]

HJELMQVIST, H. Studien über Embryologie und Variabilität bei einigen *Aphanes*-Arten. (English summary.) Bot. Not. **112**: 17–64. 1959. [*A. arvensis*, *A. microcarpa*, *A. floribunda*.]

KERSHAW, K. A. Cyclic and pattern phenomena as exhibited by *Alchemilla alpina*. Jour. Ecology **48**: 443–453. 1960.

MURBECK, S. Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Lunds Univ. Årsskr. Sect. 2 **36**(7): 1–46. *pls. 1–6*. 1901.

———. Über das Verhalten des Pollenschlauches bei *Alchemilla arvensis* (L.) Scop. und das Wesen der Chalazogamie. *Ibid*. **36**(9): 1–20. *pls. 1, 2*. 1901.

———. Zur Morphologie und Systematik der Gattung *Alchemilla*. *Ibid*. II. Sect. 2. **11**(8): 1–16. 1915.

PERRY, L. M. A tentative revision of *Alchemilla* § *Lachemilla*. Contr. Gray Herb. **84**: 1–57. 1929.

REICHGELT, T. *Aphanes microcarpa* in the Netherlands. Acta Bot. Neerl. **1**: 115–121. 1952. [Discusses distinctions between *A. microcarpa* and *A. arvensis*; also reasons for generic status of *Aphanes*.]

ROTHMALER, W. Systematische Vorarbeiten zu einer Monographie du Gattung *Alchemilla* (L.) Scop. emend. III. Notizen uber das Subgenus Aphanes (L.). Repert. Sp. Nov. **38**: 36–43. 1935. VII. Aufteilung der Gattung und Nomenklatur. *Ibid*. **42**: 164–173. 1937. [*Alphanes* recognized at generic level, list of species and their distributions.]

———. Aufforderung zur Mitarbeit an einer Flora von Europa. (Introduction à une Flore d'Europe). Repert. Sp. Nov. **53**: 254–270. 1944. [Textbeispiel eines Manuskripte für die "Flora Europaea." (Exemple de manuscript pour la "Flora Europaea"); *Aphanes*, 265–270.]

TURESSON, G. Variation in the apomictic microspecies *Alchemilla vulgaria* L. Bot. Not. **1943**: 413–427. 1943. II. Progeny tests in agamotypes with regard to morphological characters. *Ibid*. **109**: 400–404. 1956. III. Geographical distribution and chromosome number. *Ibid*. **110**: 413–422. 1957.

WALTERS, S. M. The taxonomic implications of apomixis. Pp. 162–168. *In*: J. G. HAWKES, *ed*., Reproductive biology and taxonomy of flowering plants. 183 pp. *Frontisp*. Oxford. 1966.

———. Endemism in the genus *Alchemilla* in Europe. Pp. 301–305. *In*: D. H. VALENTINE, *ed*., Taxonomy, phytogeography and evolution. xi + 431 pp. London and New York. 1972.

16. **Sanguisorba** Linnaeus, Sp. Pl. 1: 116. 1753; Gen. Pl. ed. 5. 53. 1754.

Branched perennial herbs from stout rhizomes, rarely short-lived perennials or annuals from tap-roots [or shrubs]; indumentum of unicellular, multicellular, and/or glandular trichomes. Leaves basal and cauline, imparipinnately compound, long petiolate, the leaflets sessile or shortly petiolulate, toothed or deeply dissected; stipules partly sheathing the stems, those of the basal leaves adnate for their entire length to the petioles and forming membranaceous wings, those of the cauline leaves basally adnate to the petioles, the apices free and leaflet-like. Inflorescences compact to dense, long pedunculate, many flowered, indeterminate [or determinate] spikes or heads, several inflorescences terminating each stem, each flower nearly sessile, subtended by 1 bract and 2 bractlets (sometimes reduced). Flowers small, perfect or imperfect, the plants then variously monoecious.

Calyx lobes 4, somewhat petaloid, white, green, or reddish, at length deciduous; floral tube urceolate, ± 4-angled, variously textured, a nectar ring nearly closing the mouth of the tube or absent. Petals absent. Androecium of 2, 4, or to ca. 48, included or exserted stamens; filaments white or green, filiform or flattened above, long or short, not persistent; anthers didymous; pollen 6- or 3-colporate. Gynoecium of 1, 2, or rarely more carpels inclosed by, but free from, the floral tube; styles terminal, slightly or greatly exserted beyond the throat of the floral tube; stigmas much branched, the branches short to filiform; each carpel with a solitary, anatropous ovule pendulous from an adaxial placenta, the micropyle superior. Fruit accessory, of 1 or 2 hard-walled achenes inclosed within and filling the enlarged, 4-angled or 4-winged, dry, chartaceous floral tube. Seed coat thin, membranaceous; radicle superior. Base chromosome number 7. (Including *Poterium* L., 1753, and *Poteridium* Spach; *Sanguisorba* and *Poterium* first united, under the former name, by Scopoli, Fl. Carniolica ed. 2. 1: 110. 1772.) LECTOTYPE SPECIES: *S officinalis* L.; see P. A. Rydberg, N. Am. Fl. 22: 386. 1908. (Name from the Latin *sanguis*, blood, and *sobere*, to absorb, from the use of the type species as an astringent.) — BURNET.

Eighteen or more often variable species in four subgenera of the Northern Hemisphere. The genus has been studied in detail by Nordborg, and the classification used here is based on her work. Subgenus SANGUISORBA (flowers all perfect, leaflets crenate or serrate, stamens 12 or fewer) is nearly circumpolar in distribution but is absent from Greenland. Nordborg (1966) recognized two sections and five "species groups." Members of sect. SANGUISORBA (pollen 6-colporate, floral tube ± 4-angled and winged) include *S. canadensis* L., which occurs in our area, and *S. officinalis*, a broadly distributed species (circumpolar except for eastern North America and Greenland). Subgenus POTERIUM (L.) A. Br. & Bouché (flowers perfect and imperfect, the plants variously monoecious, floral tube sculptured in fruit) ranges from Europe, northern Africa, and southwestern Asia to the Himalayas; *S. minor* Scop. is naturalized in North America. Subgenus POTERIDIUM (Spach) A. Br. & Bouché (leaflets pinnatifid, stamens 4 or 2) is composed of one or two species of the south-central United States and western North America. Subgenus DENDRIOPOTERIUM (Svent.) Nordborg (shrubs, all flowers imperfect) has three species restricted to the Canary Islands and Madeira.

Sanguisorba canadensis, American burnet, a tall perennial herb with large pinnate leaves, white flowers in cylindrical, indeterminate spikes, four long-exserted stamens, and one smooth carpel per flower, occurs in moist areas frequently underlaid by peat, such as marshes, meadows, bogs, and prairies from Labrador and Newfoundland to Manitoba and Michigan, southward to New Jersey, Delaware, Ohio, Indiana, and Illinois and in the Appalachians to North Carolina. Plants with broader and shorter leaflets and sepals tinged with red and purple are found in subarctic or montane regions from Alaska to northeastern Oregon and central Idaho; these are variously recognized as a distinct species, *S. stipulata* Raf.[8] (*S. sitchensis* C. A. Meyer) or under *S. canadensis* as subsp. *latifolia* (Hooker) Calder & Taylor or var. *latifolia* Hooker.

There are similar plants in Japan, extreme eastern USSR, Siberia, Mongolia, central Asia, and Iran and Turkey. Some of these populations may be conspecific with *S. canadensis*, while others perhaps represent distinct species; see the discussions in Calder & Taylor (Fl. Queen Charlotte Islands Pt. 1. 410, 411. 1968), Fernald (Rhodora **48**: 12. 1946), Hara (Jour. Jap. Bot. **23**: 31. 1949), Hitchcock *et al.* (fam. ref.), and Nordborg (1966). *Sanguisorba canadensis* has also been reported from several localities in central Scotland from the Firth of Clyde to the Firth of Tay (see Lennie). Reported chromosome numbers for *S. canadensis*, sensu lato, are $2n = 28$ (eastern Canada, British Columbia, Alaska, Sakhalin Island, Mongolia) and $2n = 56$ (eastern Canada). It had been thought that plants from eastern North America were octoploid (and thus specifically distinct), while those from western North America and eastern Asia were tetraploid. Mulligan & Cody found, however, only tetraploids ($2n = 28$) in samples from 41 localities in Nova Scotia, New Brunswick, Quebec, and British Columbia. *Sanguisorba Menziesii* Rydb. (Alaska to the Olympic Peninsula of Washington) is somewhat intermediate between *S. canadensis* subsp. *latifolia* and *S. officinialis* and may be of hybrid origin, being either a chance hybrid or perhaps even an established amphiploid. Nordborg (1966) mentions that *S. albanica* Andr. & Jáv. from Albania is also intermediate between these same species.

Sanguisorba minor Scop. (*Poterium Sanguisorba* L.), salad or garden burnet, $2n = 28, 56$, a variable species of the Old World, is naturalized from Nova Scotia to Ontario south to North Carolina and Kentucky; it is locally adventive in Washington, Oregon, and California. Plants of this species are smaller than those of *S. canadensis*; the inflorescences are greenish, globose or slightly ovoid, and composed of both perfect (below) and functionally carpellate (above) flowers; the stamens of the perfect flowers droop and number 12 or more; there are two carpels per flower; and in fruit the floral cups are roughened between the angles. Its indigenous range is from Scandinavia to northern Africa and the Canary Islands, eastward to southwestern and central Asia. There are both tetraploid and octoploid races, the latter restricted to the Mediterranean area. Numerous segregate and allied species have been proposed. Primarily on the basis of fruit morphology (which is usually not correlated with other characters), Nordborg (1967a) recognized 5 subspecies and several "form series" of *S. minor*. Plants found in eastern North America seem to correspond to subsp. *muricata* (Spach) Nordborg. In an embryological study of this species, Nordborg (1967b) found that while only reduced embryo sacs are functional in spontaneous tetraploid and octoploid plants, there is a strong tendency toward apospory. Both amphimixis and apomixis were found in artifical tetraploid and hexaploid hybrids.

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[8] Nordborg's neotypification (Op. Bot. **11**: 54. 1966) of this name by a specimen from Japan is quite improper; Rafinesque clearly indicated that his material was from the "Oregon Mountains and territory." Also, the name was first published in Herb. Raf. 43. 1833, not in Autik. Bot. **3**: 171. 1840.)

Sanguisorba annua (Nutt. ex Hooker) Torrey & Gray, $2n = 14$, of subg. POTERIDIUM is a short-lived tap-rooted perennial or annual herb with pectinately dissected leaflets, short-cylindric inflorescences of perfect flowers, and four stamens. It occurs in disturbed habitats in the south-central United States (Arkansas, Kansas, Oklahoma, and Texas). It is locally adventive in South Carolina and Massachusetts. Clearly related plants with two stamens and with the floral cups merely four-angled at maturity, rather than four-winged, occur in the Pacific Northwest (British Columbia to California, Idaho, and Montana); these are either included in *S. annua* or recognized as a distinct species.

Pollen grains of the tetraploid and octoploid races of *Sanguisorba officinalis* differ in size and shape, and both kinds are often preserved in late-glacial deposits of northwestern Europe; fossil fruits of the species are known from the British Isles. The fossil evidence suggests that *S. officinalis* was common and widely distributed during late-glacial times, with disjunction occurring in the post-glacial period.

Sanguisorba is unusual among Rosaceae in that within the genus is found a series of morphological changes that evidently have resulted from a shift from insect to wind pollination. In the entomophilous *S. officinalis* all flowers are perfect, the inflorescences are red-purple, the stamens are short and stiff, the stigmatic branches are short and compact, and a prominent nectar ring surrounds the mouth of the floral tube. *Sanguisorba minor* is wind pollinated, as are all species of subg. POTERIUM, and the inflorescences are greenish, the stamens filiform and long exserted, the stigmatic branches quite elongate (penicillate), and a nectar ring is nearly lacking; the lower flowers of the inflorescence are perfect, while the upper ones are carpellate. Other species can have different combinations of floral characters. Both *S. canadensis* and *S. annua* have perfect flowers with long filaments and moderately long, tufted stigmatic branches. All the flowers are imperfect in the closely related anemophilous genera *Sarcopoterium* Spach (*S. spinosum* (L.) Spach, eastern Mediterranean area) and *Bencomia* Webb & Berth. (four species of the Canary Islands and Madeira); plants of the former are monoecious, those of the latter dioecious.

Sanguisorba, *Sarcopoterium*, and *Bencomia* constitute the "*Sanguisorba* group" of Nordborg. Allied genera are *Margyricarpus* Ruiz & Pavon (two or more species of Andean South America and the Juan Fernández Islands); *Tetraglochin* Poeppig (possibly eight species of the Andes, often included in the preceding genus); *Acaena* L. (about 40 species, circum-Antarctic: Australia, Tasmania, New Zealand, islands of the southern Indian and Atlantic Oceans, South Africa, Hawaii, Patagonian and Andean South America northward to California); *Polylepis* Ruiz & Pavon (about 20 species, Andean South America); and *Cliffortia* L. (80 species of South Africa with one in East Africa, Nyassaland, and Angola). A natural intergeneric hybrid is × *Margyracaena Skottsbergii* Bitter (*Acaena argentea* Ruiz & Pavon × *Margyricarpus digynus* (Bitter ex Skottsb.) Skottsb.)

from the Juan Fernández Islands. These genera are of particular interest because of their geographical distribution, often bizarre growth habits, frequent occurrence of imperfect flowers and wind pollination, and adaptations for dispersal by animals or wind.

REFERENCES:

Under family references see BATE-SMITH, BOUTINEAU, BUNTING, CHITTENDEN, HEGI, LUBBOCK, RICKETT, ROSS-CRAIG, and WOOD.

BERGLUND, B. E. Late-Quaternary records of *Sanguisorba officinalis* in southeastern Sweden. Bot. Not. **116:** 289–292. 1963.

BÖCHER, T. W., & K. LARSEN. Cytotaxonomical studies in the *Sanguisorba minor* complex. Bot. Tidsskr. **53:** 284–290. 1957.

ERDTMAN, G., & G. NORDBORG. Über Möglichkeiten die Geschichte verschiedener Chromosomenzahlenrassen von *Sanguisorba officinalis* und *S. minor* pollenanalytisch zu beleuchten. Bot. Not. **114:** 19–21. 1961.

GODWIN, H. The history of the British flora. A factual basis for phytogeography. viii + 384 pp. *26 pls. Chart.* Cambridge, England. 1956. [*Poterium* and *Sanguisorba*, 118, *pl. 23*; fossil fruit and pollen remains.]

LARSEN, K. Chromosome studies in some Mediterranean and South European flowering plants. Bot. Not. **109:** 293–307. 1956. [*Bencomia*, *Dendriopoterium*, *Marcetella*, discussion of Sanguisorbeae.]

———. Cytology of the genus *Sanguisorba.* Nature **184:** 743, 744. 1959.

LENNIE, J. M. *Sanguisorba canadensis* at Castle Semple Loch. Glasgow Nat. **18:** 522. 1967. [Also see the editor's note that follows.]

LINDENBEIN, W. Beiträge zur Kenntnis der Samen und Früchte. I. *Sanguisorba minor* Scop. und *S. muricata* (Spach) Greml. Ang. Bot. **30:** 107–119. 1956.*

MULLIGAN, G. A., & W. J. CODY. A clarification of the chromosome number situation in *Sanguisorba canadensis.* Canad. Jour. Bot. **51:** 2075–2077. 1973.

——— & ———. Rosaceae, p. 194. *In:* Á LÖVE, IOPB Chromosome number reports XLIII. Taxon **23:** 193–196. 1974. [*S. minor*, $2n = 56$; *S. occidentalis*, $2n = 14$; *S. officinalis* subsp. *microcephala*, $2n = 28$.]

NORDBORG, G. Studies in *Sanguisorba officinalis* L. Bot. Not. **116:** 267–288. 1963.

———. *Sanguisorba* L., *Sarcopoterium* Spach, and *Bencomia* Webb et Berth. Delimitation and subdivision of the genera. Op. Bot. **11**(2): 1–103. *pls. 1–6.* 1966.

———. The genus *Sanguisorba* section *Poterium.* Experimental studies and taxonomy. *Ibid.* **16:** 1–166. 1967a.

———. Embryological studies in the *Sanguisorba minor* complex (Rosaceae). Bot. Not. **120:** 109–119. 1967b.

———. Pubescence in the *Sanguisorba* group (Rosaceae). *Ibid.* **121:** 641–651. 1969.

PHELOUZAT, R. Ontogénie de la pousse aérienne chez le *Poterium Sanguisorba* L. Compt. Rend. Acad. Sci. Paris **255:** 153–155. 1962.

———. Morphologie, phyllotaxie, ontogénie de trois Rosacées: *Agrimonia Eupatoria* L., *Poterium Sanguisorba* L., *Geum urbanum* L. Revue Cytol. Biol. Vég. **26:** 101–362. 1963.*

———. La gamétogénèse et la fertilité dans les fleurs femelles et les fleurs hermaphrodites du *Poterium Sanguisorba* L. Bull. Soc. Bot. France **112:** 370–378. *pls. 1, 2.* 1965.

PIROLA, A. Ricerche su *Sanguisorba dodecandra* Moretti. (English summary.) Ist. Bot. Univ. Lab. Crittog. Pavia Atti V. **21**: 69–103. 1964. [Includes photographs and good illustrations.]

REITSMA, T. Some aspects of the pollen morphology of the genus *Sanguisorba* L. (Rosaceae). Rev. Paleobot. Palynol. **4**: 305–310. 1967. [Reprinted as Meded. Bot. Mus. Herb. Rijksuniv. Utrecht **293**. 1967.]

VAHL, I. On germination inhibitors. III. Germination inhibitors in the fruits of *Poterium spinosum* L. Palestine Jour. Bot. Jerusalem **2**: 28–32. 1940.

WEIMARCK, H. Monograph of the genus *Cliffortia*. 233 pp. Lund. 1934. [Discussion of relationships of *Cliffortia* and its relatives, 176–186.]

(*To be concluded*)